



Impact of a shared sugar food source on biological control of *Tuta absoluta* by the parasitoid *Necremnus tuta*

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Received: 2 November 2018 / Revised: 28 August 2019 / Accepted: 19 October 2019 / Published online: 7 November 2019
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Abstract

Honeydew is a sugar-rich food source produced by sap-feeding insects, notably by major pests such as aphids and whiteflies. It is an important alternative food source for the adult stage of various key natural enemies (e.g., parasitoids), but it may be used also as food by agricultural pests. *Necremnus tuta* is an idiobiont parasitoid, and it is the most abundant larval parasitoid associated with the South American tomato pinworm, *Tuta absoluta*, in recently invaded European areas. The impact of *N. tuta* on *T. absoluta* populations was evaluated under greenhouse conditions with and without the presence of a honeydew producer, the aphid *Macrosiphum euphorbiae*. In addition, laboratory experiments were performed to evaluate the longevity of *N. tuta* and *T. absoluta* adults when fed with water, honey or honeydew produced by the aphid. In the greenhouse, *N. tuta* effectively reduced *T. absoluta* population by the end of the experiment, and this independently of the presence of the aphid; still the presence of *M. euphorbiae* led to delayed and reduced *T. absoluta* population peak when controlled by the parasitoid (there was a fourfold increase in parasitoid density in presence of aphid). The longevity of both *N. tuta* and *T. absoluta* females increased in the presence of honeydew (when compared to water only) under laboratory conditions; it hinted that honeydew could be used by an herbivore as *T. absoluta*. The interactions between the two phytophagous species showed contrasting effects, and this mostly independently of parasitoid presence. *Tuta absoluta* had no impact on aphid population dynamics. By contrast, the production of *T. absoluta* larvae was higher in the first part of the experiment as the adults lived longer (feeding on aphid honeydew) and produced more larvae. In the second part of the experiment, there were fewer *T. absoluta* larvae in the presence of the aphid, likely owing to resource competition and/or negative plant-mediated indirect interactions. We demonstrated that honeydew producers could impact parasitoid-host population dynamics both through direct and indirect interactions and that potential positive effects of a sugar food source toward a pest can be nullified in the long term by other negative effects occurring simultaneously.

Keywords Eulophidae · Biological control · Solanaceae · Gelechiidae · Honeydew

Key messages

- The parasitoid *Necremnus tuta* suppressed *T. absoluta* population growth with and without aphid under greenhouse conditions.
- Honeydew increased *N. tuta* and *T. absoluta* adult longevity both under laboratory and greenhouse conditions.
- Aphid presence led to delayed and reduced *T. absoluta* population peak when controlled by *N. tuta*.
- *Necremnus tuta* had no impact on aphid population growth despite effective biological control of the other herbivore (*T. absoluta*).
- Honeydew producer could impact parasitoid-host population dynamics through direct and indirect interactions.

Communicated by M. Traugott.

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Introduction

The South American tomato pinworm, *Tuta absoluta* Meyrick (Lepidoptera: Gelechiidae), is considered one of the main agricultural threats to world tomato production (Desneux et al. 2010, 2011; Biondi et al. 2018). *Tuta absoluta* was first observed outside South America in Eastern Europe in 2006 and spread rapidly throughout Africa, the Middle East and parts of Asia (Campos et al. 2017; Sankarganesh et al. 2017; Han et al. 2018, 2019; Mansour et al. 2018; McNitt et al. 2019), as well as in central America in a lesser extent (Biondi et al. 2018; Verheggen and Fontus 2019). Chemical control is the method used most to prevent the outbreaks of *T. absoluta* in newly invaded areas due to the lack of effective alternatives (Biondi et al. 2018). However, insecticide efficiency may be compromised due to the cryptic nature behavior of the larvae that mine leaves, and occasionally stems, flowers and tomatoes (Guedes and Picanço 2012). Moreover, wide use of insecticides can cause extensive side effects, such as the development of resistance to insecticides in *T. absoluta* populations (Campos et al. 2015; Roditakis et al. 2018; and see Guedes et al. 2019) as well as a detrimental impact on non-target organisms such as natural enemies (Lu et al. 2012; Biondi et al. 2015; Jam and Saber 2018; Mohammed et al. 2018; Passos et al. 2018; Soares et al. 2019a, b) through multiple potential sublethal effects (Desneux et al. 2007). Indeed, an alternative to conventional pest control is to increase the activity of naturally occurring enemies within integrated pest management (IPM) programs (Ragsdale et al. 2011; Biondi et al. 2018; Perovic et al. 2018; Jactel et al. 2019).

Several predators and parasitoids spontaneously attacking *T. absoluta* in tomato crops in Europe have been identified (Castañé et al. 2011; Mollá et al. 2011; Zappalà et al. 2013). However, in tomato systems, *T. absoluta* coexist with a large number of pests including aphids, whiteflies and fruit worms (Kennedy 2003), that may indirectly interact with potential biological control agents in complex food webs. Indirect interaction is an important force driving insect communities, species density and diversity, including direct and indirect effects inside and outside the agroecosystem (van Veen et al. 2005). Indirect interactions may occur (i) between two prey or host species sharing the same natural enemy through predation or parasitization, and (ii) between two species separated in time or space and interacting in different ways with natural enemies (Chailleux et al. 2014b). Among the other pests present in the tomato systems, aphids such as *Macrosiphum euphorbiae* Thomas (Hemiptera: Aphididae: Macrosiphini) have been described as pests able to produce honeydew (Hullé et al. 2019). Honeydew is a carbohydrate-rich source that may

be used as a food source by adults of natural enemies and phytophagous pests to enhance their fitness (Wäckers et al. 2008). Hence, the availability of suitable food sources (e.g., intrinsic plant quality in terms of nutritional status, and other alternative food sources) could affect the outcome of pest-natural enemy interactions and may be critical for the efficiency of biological pest control (Bompard et al. 2013, Chailleux et al. 2014b; Jaworski et al. 2015; Biondi et al. 2016; Desneux et al. 2019). The study of the multitrophic interactions among natural enemies and invasive pests is required to design effective biological control within the framework of the tomato management program.

Augmentative biological control relies on periodic releases of natural enemies that mainly attack eggs and other small arthropod instars (Desneux et al. 2010; Chailleux et al. 2013; Zappalà et al. 2013). However, other biological control agents that impact different pest stages, mainly in *T. absoluta*, as well as in different phenological stage and architecture of tomato plants have to be implemented (Perdikis et al. 2014; Mirhosseini et al. 2019). The eulophid parasitoid *Necremnus tutae* Ribes & Bernardo (Hymenoptera: Eulophidae) has been observed and is widespread in Europe and Africa parasitizing *T. absoluta* (Gebiola et al. 2015). It has been identified as a promising biological control agent on *T. absoluta* (Biondi et al. 2013a; Chailleux et al. 2014a; Naselli et al. 2017; Bodino et al. 2019). Previous laboratory trials showed that *N. tutae* reproductive and longevity outcomes were enhanced by the simultaneous presence of the sap feeder *Bemisia tabaci* Gennadius (Hemiptera: Aleyrodidae), a honeydew producer (Dong et al. 2018). However, more field studies are needed to test the ability to control pest population.

In this context, we assessed the effect of the aphid presence on both *T. absoluta* and *N. tutae* population dynamics in a greenhouse experiment (i) to confirm the potential role of *N. tutae* as biological control agent of *T. absoluta*; and (ii) to test the impact of the presence of the honeydew, as a sugar food source, on parasitoid longevity and its ability to control the pest population. In addition, we tested the impact of honeydew as a food source for these two insects on the parasitoid longevity in a laboratory experiment.

Materials and methods

Biological material

Tomato plants cv. Nano were grown in a climatic chamber until the seedlings emerged (25 ± 3 °C, $65 \pm 5\%$ relative humidity [RH] and a photoperiod of 16:08 [L:D] h) in cubic plastic pots ($7 \times 7 \times 6.5$ cm). After emergence, the tomato seedlings were placed under greenhouse conditions (20 ± 2 °C, $65 \pm 5\%$ RH and a photoperiod of 10:14 [L:D]

Table 1 Sampling protocol schedule including plant growth (S=plant seeding; T1/T2= plant handling events), and plant sampling events (A=assessment)

Species	Days after seeding (DAS)														
	0	6	23	30	34	44	45	64	71	78	85	92	99	106	113
<i>Solanum lycopersicum</i>	S	T1	T2							A	A	A	A	A	A
<i>Tuta absoluta</i>				R			R								
<i>Macrosiphum euphorbiae</i>					R										
<i>Necremnus tuta</i>						R		R							

Tuta absoluta adults (n=20 couples), *M. euphorbiae* adults (n=5 aphids/tomato plant) and *N. tuta* adults (25 couples) infestation (R: release time) and development throughout the plant development stages. The assessment started 71 days after seeding (DAS) to DAS 113

h). At 6 days after seeding (DAS), the tomato seedlings were washed to remove soil and then transferred to new pots containing inert substrate (Perlite Italiana srl, Corsico, Italy) (see schedule Table 1). At DAS 24, the plants were transferred to larger pots (diameter: 10 cm, height: 9 cm) filled with the same substrate and placed in four separate compartments in the greenhouse. All the plants were watered using nutrient solution, and the latter was adapted for all the treatments to pH 6.0 ± 0.2 by using H₂SO₄ (0.2 M) according to the compartment.

The *T. absoluta* colony was maintained in cages (55 × 75 × 80 cm), in regular chambers using pesticide free potted tomato plants (Biondi et al. 2013b). A solution containing 10% honey was provided ad libitum to adults in rearing cages. The *N. tuta* parasitoids originated from field-collected material and were reared in cages (45 × 45 × 55 cm) on *T. absoluta* kept on tomato plants in a climatic chamber. The *M. euphorbiae* aphid colony was maintained in a cage (90 × 50 × 60 cm) placed in the greenhouse using tomato plants as host (22 ± 5 °C, 60 ± 10% [RH] and during a photoperiod of 15:09 [L:D] h).

Greenhouse experiment

The experiment was performed at the French National Institute for Agricultural Research (INRA), Sophia Antipolis, France, in 2016 and 2017. The performance of *N. tuta* was checked with and without the honeydew produced by *M. euphorbiae* in semi-field. The experiment was carried out in the greenhouse in four separated glass compartments. Each compartment had eight rows, and every row was composed of eight tomato plants (Fig. 1). Four tunnels were created for the treatments and consisted in 16 tomato plants that were covered with slim nylon mesh (5 × 1 × 2 m). The following four treatments were set up: (i) *T. absoluta* (negative control), (ii) *T. absoluta* + *M. euphorbiae*, (iii) *T. absoluta* + *N. tuta* (iv) *T. absoluta* + *M. euphorbiae* + *N. tuta* (Fig. 1). The treatments described above were replicated four times in each greenhouse compartment. A general overview of the experiment design is shown in Table 1. The first release was performed with 20 couples of *T. absoluta* in 30 DAS in all treatments (i–iv). 34 DAS, five *M. euphorbiae* were placed on top of each tomato plant in treatments (iii) and (iv). 44

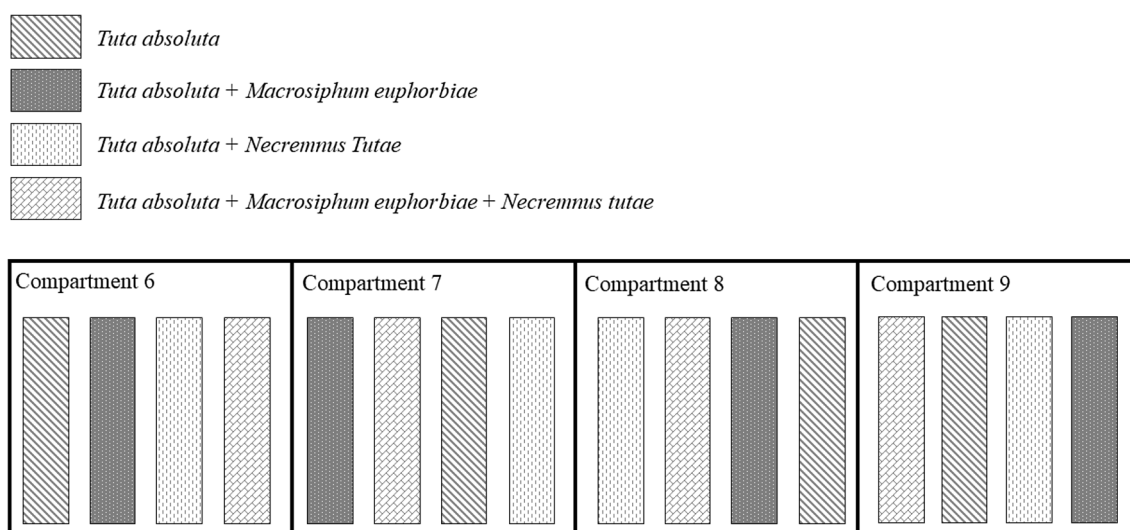


Fig. 1 Experimental design framework. Each compartment was divided into four treatments. All treatments had two rows with 16 tomato plants covered with slim nylon mesh

DAS, 25 couples of *N. tutae* were released in treatments (ii) and (iv). Likewise, in the second release, 20 couples of *T. absoluta* were again released at 45 DAS. The second parasitoid release was performed at 64 DAS with 25 couples of *N. tutae* in treatments (ii) and (iv). The assessments started one week after the second release at 71 DAS. The assessments were carried out randomly on four tomato plants for each treatment, on 16 tomato plants weekly. Two tomato leaves were surveyed on the top, middle and at the bottom of tomato plants. The number of *T. absoluta* larvae and adults, *N. tutae* adults and *M. euphorbiae* (nymphs and adults) was counted.

Laboratory experiment

Honeydew collection. The honeydew was collected using parafilm (plastic packaging, Chicago, IL) strips in the *M. euphorbiae* colony reared on tomato plant. The parafilm was exposed for 24 h under the tomato leaves with high *M. euphorbiae* density. Once the parafilm strips were removed, the abundance of honeydew was checked using a stereoscope microscope (20x), and thereafter placed inside Petri dishes for storage at $-12\text{ }^{\circ}\text{C}$ until needed.

***Necremnus tutae* and *T. absoluta* survival.** The experiment was performed to verify *N. tutae* female parasitoid survival. Three treatments were designed: (i) *N. tutae* + water (control), (ii) *N. tutae* + honey and (iii) *N. tutae* + honeydew. The same procedure was carried out with *T. absoluta* females. The parafilm was cut into strips (1 cm \times 5 cm) containing honeydew, honey or water. For each treatment, a parafilm strip was inserted into a glass tube (3 cm diameter \times 10 cm height) and the latter was closed using moistened cotton. Then, a 24-h-old female *N. tutae* or *T. absoluta* was introduced into this tube which was placed in the thermostatic cabinet ($25 \pm 1\text{ }^{\circ}\text{C}$, $60 \pm 10\%$ [RH] for a photoperiod of 16:08 [L:D] h), and checked daily to determine insect survival.

Statistical analysis

The statistical analyses were performed using R version 3.4.0. The impact of the treatments (with or without *N. tutae*) and of the time period (number of days after seeding) on the number of *M. euphorbiae* was analyzed using a linear mixed model with the treatments and the time as fixed effects and the compartment number as a random effect (the dependent variable follows a normal distribution confirmed by a Shapiro–Wilk test). Moreover, the impact of the treatments on each sampling day on the number of aphids was analyzed using the same method as described above. The impact of the treatments (T, TM, TMN, TN) and of the time period (number of days after seeding) on the number of *T.*

absoluta larvae and adults, as well as the number of *N. tutae* adults, was analyzed using a generalized linear mixed model following a Poisson distribution. This model was built using the treatments and the time as fixed effects and the compartment number as a random effect. The impact of the treatments on each sampling day on the number of *T. absoluta* larvae and adults and *N. tutae* was analyzed using the same method as described above. Whenever necessary, a multi-comparison test was done, using the package multcomp. A log-rank test and the Holm–Sidak multiple comparison procedure were used to identify significant differences among the survival curves of *T. absoluta* and *N. tutae* adults fed with water, honeydew produced by *M. euphorbiae* or honey. The figures were obtained using SigmaPlot v.12.5 (Systat Software Inc. 2011).

Results

Greenhouse experiment

The number of *T. absoluta* larvae depended on the different treatments ($\chi^2_3 = 67.2$, $P < 0.001$) and the sampling day ($\chi^2_6 = 162.9$, $P < 0.001$) (Fig. 2). The number of *T. absoluta* larvae was stable the first 85 DAS and in the assessments of 99–106 DAS; it increased between the 92 and 99 DAS; and it finally decreased between the 106 and 113 DAS. Taking into consideration each sampling day, the number of larvae in the treatment with *T. absoluta* only was the lowest until 92 DAS. Then, the number of *T. absoluta* larvae increased until 113 DAS, with a population peak at the 106 DAS (Table 2, Fig. 2). In the treatment with *M. euphorbiae*, the number of *T. absoluta* larvae was higher at the beginning of the assessments and decreased after 78 DAS. However, after 85 DAS the number of *T. absoluta* larvae increased gradually until the end of the assessments, reaching a density almost twofold lower than when *T. absoluta* was alone. The treatment with only the parasitoid *N. tutae* showed a population peak of *T. absoluta* larvae at 92 DAS and then a decrease until 113 DAS, reaching a very low level by the end of the experiment. In the treatment with the three species, the population dynamic of *T. absoluta* was similar but showed lower and delayed population peak density (at 99 DAS) as well as lower larvae densities by the end of the experiment (106–113 DAS) (Fig. 2).

The number of *T. absoluta* adults depended on the various treatments ($\chi^2_3 = 56.6$, $P < 0.001$) and the sampling day ($\chi^2_6 = 391.9$, $P < 0.001$) (Fig. 3). The numbers of *T. absoluta* adults were similar the two first weeks (71 and 78 DAS). Then they increased slightly between 85 and 92 DAS and then increase steadily by the end of the experiment. The number of *T. absoluta* adults was not statistically different

Fig. 2 Mean (\pm SEM) number of *Tuta absoluta* larvae per tomato leaf per week in four different treatments (*T. absoluta* only, *N. tutae* + *T. absoluta*, *M. euphorbiae* + *T. absoluta* and *N. tutae* + *T. absoluta* + *M. euphorbiae*). GLM following a Poisson distribution was used to compare the number of *T. absoluta* larvae among treatments at each sampling date. Mean number under the same small letters is not significantly different at each sampling day among treatments

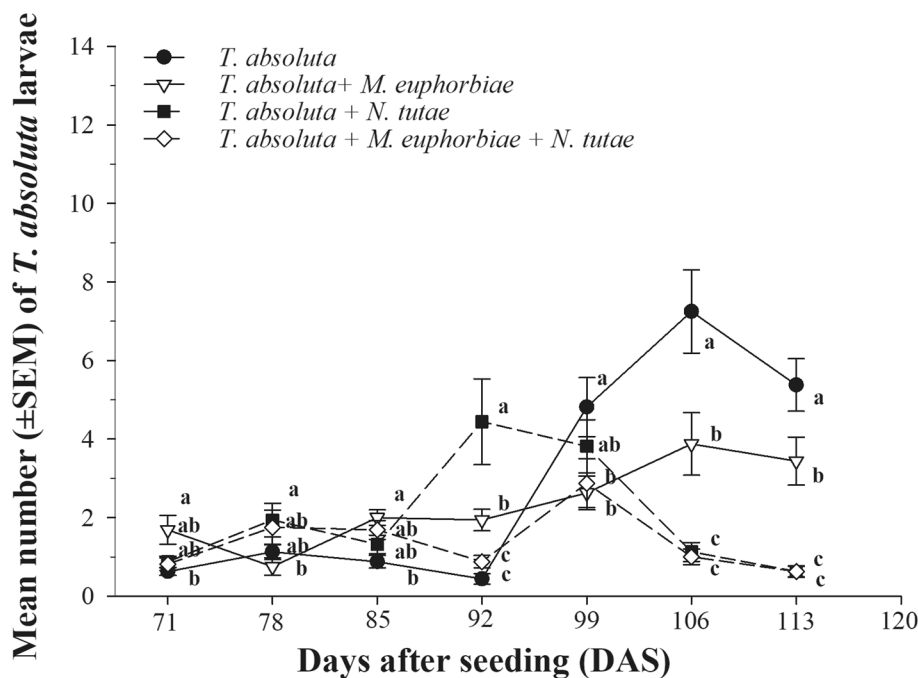


Table 2 Statistical results of the effects of the treatments (*Tuta absoluta* with or without *Necremnus tutae* and/or *Macrosiphum euphorbiae*) on the number of *T. absoluta* (larvae and adults), parasitoids as well as aphids per tomato leaf at each sampling day

Days after release	Mean number of <i>T. absoluta</i> larvae			Mean number of <i>T. absoluta</i> adult			Mean number of <i>N. tutae</i> adult			Mean number of <i>M. euphorbiae</i>		
	χ^2	Df	P value	χ^2	Df	P value	χ^2	Df	P value	F value	Df	P value
71	9.7	3	0.021	4.4	3	0.225	1.4	1	0.239	1.5	1, 30	0.235
78	9.7	3	0.021	22.4	3	<0.001	0.1	1	0.839	0.5	1, 30	0.486
85	8.7	3	0.034	19.6	3	<0.001	1.4	1	0.239	0.2	1, 30	0.652
92	76.6	3	<0.001	10.0	3	0.018	15.3	1	<0.001	1.8	1, 30	0.193
99	13.2	3	0.004	35.8	3	<0.001	3.9	1	0.045	0.2	1, 30	0.687
106	123.9	3	<0.001	6.6	3	0.085	4.8	1	0.028	1.3	1, 30	0.263
113	109.2	3	<0.001	37.3	3	<0.001	5.1	1	0.024	20.0	1, 30	0.165

Significant effects of the treatments on the *T. absoluta*, *N. tutae* or *M. euphorbiae* are indicated in bold text

among the treatments at 71 to 78 DAS and at 106 DAS (Table 2 and Fig. 3). The number of *T. absoluta* adults in the treatments with only *M. euphorbiae* + *T. absoluta* was higher than in the treatment *T. absoluta* alone (i.e., without *M. euphorbiae*) and with the three species at 99 DAS. Nevertheless, at 113 DAS in the end of the experiment, the number of *T. absoluta* adults was highest in the treatment with *M. euphorbiae* (Fig. 3).

The number of the parasitoid *N. tutae* depended on the presence of *M. euphorbiae* ($\chi^2_1 = 12.7, P < 0.001$) and on the sampling day ($\chi^2_6 = 37.5, P < 0.001$) (Fig. 4). The number of *N. tutae* adults was stable the first 85 DAS and between 106 and 113 DAS; it increased between 85 and 92 DAS and at 99–106 DAS; and then it finally decreased between 92 and 99 DAS. The number of *N. tutae* was not statistically different in the first three assessments at 71–85 DAS (Table 2 and Fig. 4). However, in the treatment with *M. euphorbiae* the

number of *N. tutae* was threefold–fourfold higher than the treatment without *M. euphorbiae* at 85–113 DAS (Fig. 4).

The number of *M. euphorbiae* was not strongly impacted on the presence of *N. tutae*, although marginally significantly with slightly higher aphid number by the end of the experiment when the parasitoid was present ($F_{1214} = 3.5, P = 0.065$). The main factor was impacting aphid density was sampling day ($F_{1214} = 30.3, P < 0.001$) (Table 2, Fig. 5). The number of aphids increased on 85–99 DAS, and it was similar to the assessments at 71–85 DAS as well as those at 99–113 DAS.

Laboratory experiment

Tuta absoluta adult survival was impacted by the food source provided (log-rank test: $\chi^2 = 1462.424, df = 2, P < 0.001$) (Fig. 6a). All the survival curves were significantly different

Fig. 3 Mean (\pm SEM) number of *Tuta absoluta* adults per tomato leaf per week in four different treatments (*T. absoluta* only, *N. tutae* + *T. absoluta*, *M. euphorbiae* + *T. absoluta* and *N. tutae* + *T. absoluta* + *M. euphorbiae*). GLM following a Poisson distribution was used to compare the number of *T. absoluta* adults among treatments at each sampling date. Mean number under the same small letters is not significantly different at each sampling day among treatments

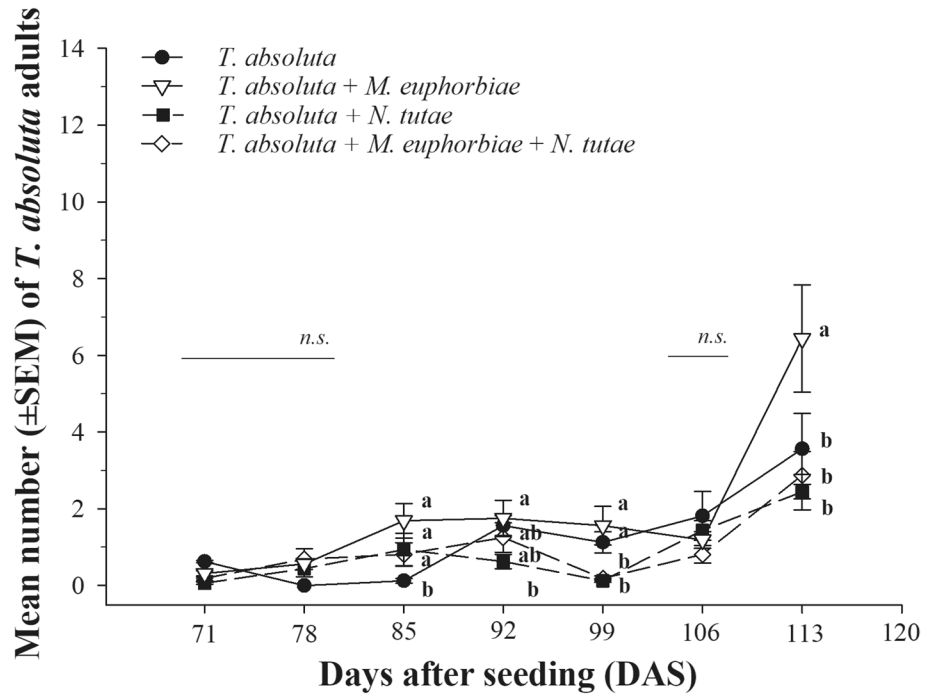


Fig. 4 Means (\pm SEM) number of *Necremnus tutae* adults per tomato leaf per week in four different treatments per week in two different treatments (with and without *M. euphorbiae*). GLM following a Poisson distribution was used to compare the number of *N. tutae* adults among treatments at each sampling date. Mean number under the same small letters is not significantly different at each sampling day among treatments

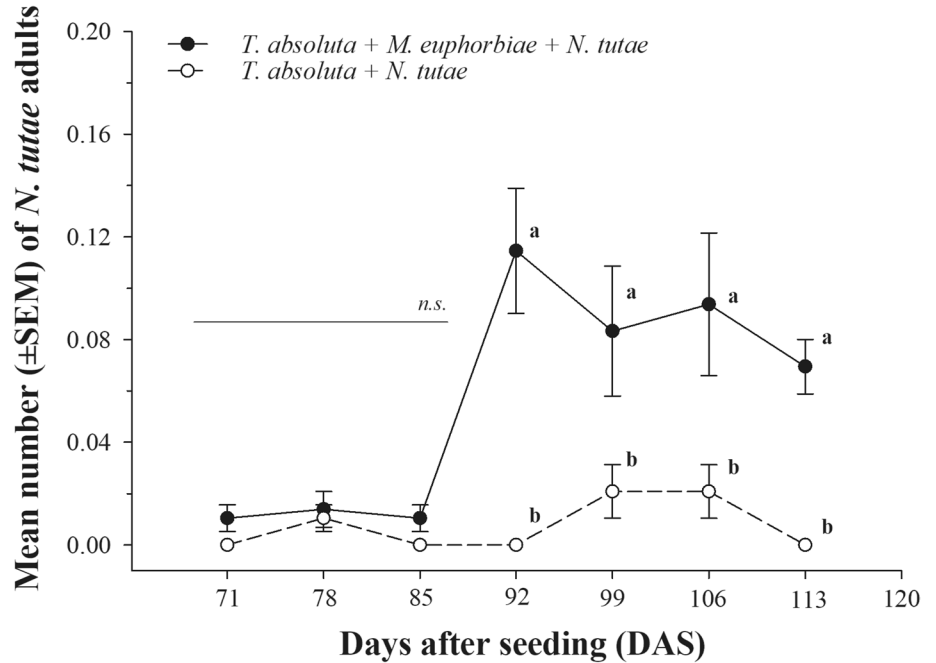


Fig. 5 Mean (\pm SEM) number of *Macrosiphum euphorbiae* per tomato leaf per week in two different treatments (with and without *Necremnus tuta*). A linear regression was used to compare the number of *M. euphorbiae* among treatments at each sampling date

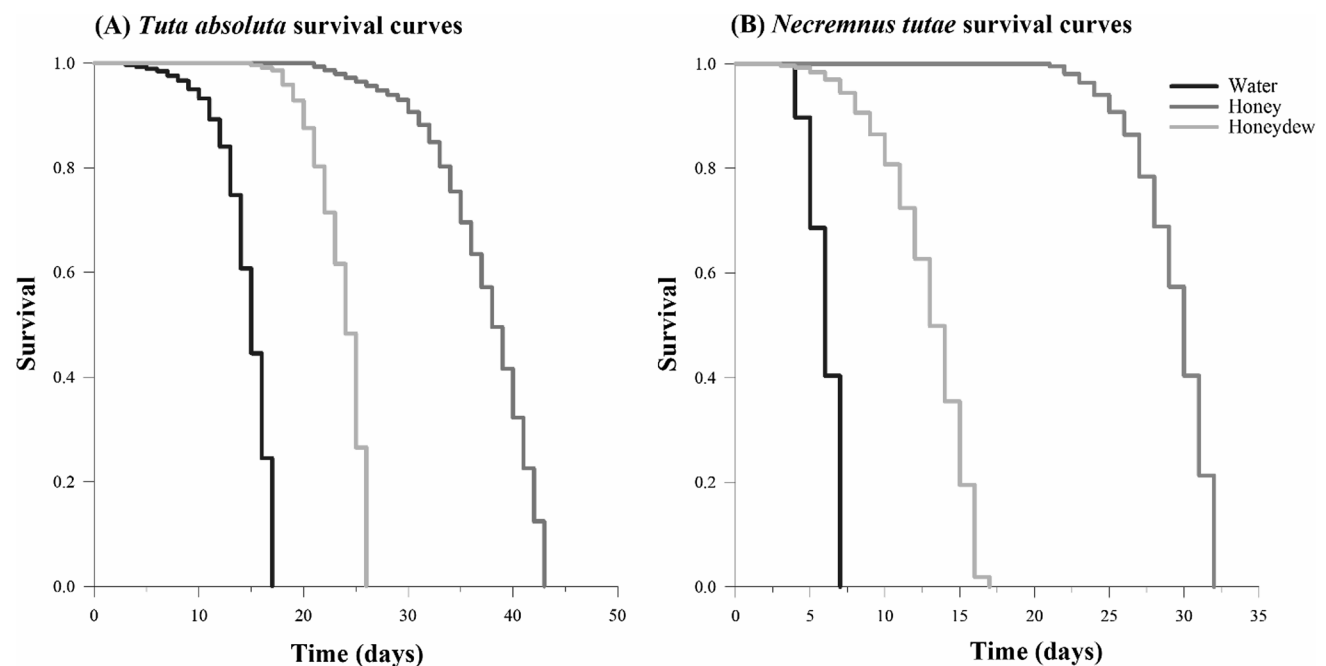
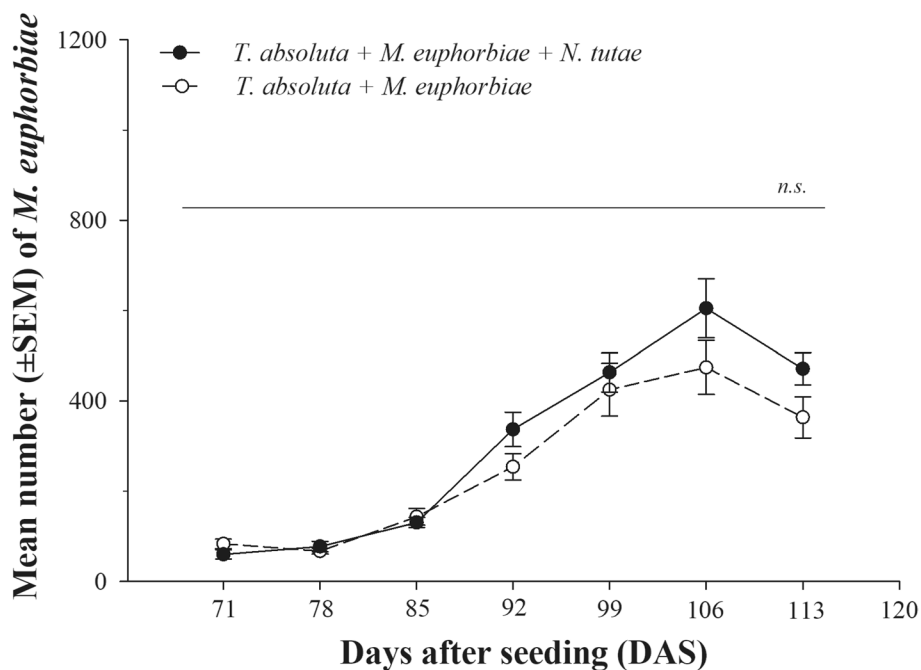


Fig. 6 Survival curves of **a** *Tuta absoluta* and **b** *Necremnus tuta* female adults fed in three different treatments with water, honey or honeydew. The survival curve was significantly different according to Holm–Sidak’s test ($P < 0.05$)

with the Holm–Sidak test ($P > 0.05$). The survival of the parasitoid *N. tuta* females was also impacted by the food source provided (log-rank test: $\chi^2 = 1222.04$, $df = 2$, $P < 0.001$) (Fig. 6b). All the survival curves were significantly different with Holm–Sidak test ($P > 0.05$).

Discussion

The importance of sugar food sources in biological control program has been largely reported in light of their positive effects on biocontrol agents (Wäckers et al. 2008; Tena

et al. 2018; Heimpel 2019; Picciau et al. 2019; Monticelli et al. 2019); still the impact that such food sources may have on herbivorous pests has been scarcely documented (Wäckers et al. 2007; Winkler et al. 2009). Honeydew is the most commonly available sugar food source in agricultural systems (Wäckers et al. 2008) and is produced by sap-feeding insects, including by pests such as aphids and whiteflies (Hendrix et al. 1992; Hullé et al. 2019). In tomato crops, the biological control of the major pest *T. absoluta* by the parasitoid *N. tutae* may be modulated by honeydew presences as tomato plants are often infested by whiteflies and/or aphids. The *N. tutae* parasitoid provided effective biological control of *T. absoluta*, and this regardless of aphid presence (*M. euphorbiae*). However, the aphid presence had various effects on the system (i) the peak population of *T. absoluta* was both delayed and reduced when controlled by the parasitoid, (ii) *T. absoluta* adults fed with aphid honeydew lived longer, stressing that honeydew food source could be used positively by an herbivore, and more larvae were produced in first part of greenhouse experiment, (iii) in the second part, there were fewer *T. absoluta* larvae potentially owing to occurrence of resource competition and/or plant-mediated indirect interactions with the aphid. The present study hinted that honeydew producers may impact parasitoid-host population dynamics both through direct and indirect interactions and that potential positive effects of a sugar food source toward a pest can be nullified in the long term by other negative effects occurring simultaneously. Analyzing these interactions may provide data on the potential role of biological control agents on key pests in the framework of IPM in greenhouse tomato crops.

Impact of honeydew

Necremnus tutae is a synovigenic parasitoid species, i.e., females continuously mature eggs throughout their lifespan relying both on their own nutritional reserves and on additional nutrients acquired, for example, through host feeding (Jervis et al. 2001; Balzan and Wäckers 2013). In addition to feeding on host hemolymph, parasitoid females require sugar food sources such as floral nectar and/or honeydew in order to sustain biological traits linked to actual parasitoid fitness (Jervis et al. 2001; Wäckers et al. 2008; Benelli et al. 2017). Honeydew consumption has been shown to increase parasitoid longevity (Hogervorst et al. 2007; Hagenbucher et al. 2014; Tena et al. 2018) and may be involved in parasitoid performance, e.g., by increasing offspring production (Lahiri et al. 2017; Dong et al. 2018; Picciau et al. 2019); this has notably been reported for *N. artynes* feeding on floral nectar (Balzan and Wäckers 2013) as well as for *N. tutae* feeding on whitefly honeydew (Dong et al. 2018). We demonstrate further that tomato aphid honeydew enhances *N.*

tutae adult longevity under laboratory conditions (Fig. 6b); the presence of honeydew producers in greenhouse however provided positive effects on parasitoid longevity, although this effect was confounded with potential positive impact on parasitoid fecundity (Fig. 4. DAS 92–113).

In addition to its impact on parasitoid, honeydew also proved as a potential reliable sugar food source for *T. absoluta* adults notably increasing their longevity under laboratory conditions (Fig. 6a); it was also suggested by the greenhouse experiment when comparing *T. absoluta* alone vs. *T. absoluta* + aphid (significantly higher *T. absoluta* density in DAS 85, 99 and 113, Fig. 3). Still this positive effect of aphid honeydew on adults was offset in the long term by the multiple negative effects that pullulating aphids have on *T. absoluta* larvae (see below). In addition, it is known that lifespan increase does not cascade directly to fitness increase in lepidopterans (Jervis et al. 2007), as demonstrated for *T. absoluta* for which 97% of realized fecundity occurs in first 17 days (Lee et al. 2014). As honeydew led to an increase in *T. absoluta* longevity from 17 days (water only) to 26 days (honeydew), such increase could only provide marginal increase in fecundity. Honeydew still may provide other benefits to *T. absoluta* adults as rich-sugar food sources could enhance lepidopterans mobility and thus dispersion (Jervis et al. 2007).

Effects of the secondary pest on biotic interactions at play in the system

Various biotic interactions are usually at play in complex agroecosystems involving multiple arthropod pests and natural enemies, thus identifying potential mechanisms underneath and the demographic consequences of such key interactions is crucial for increasing both applied and fundamental knowledge (Chailleux et al. 2014b; Naselli et al. 2017). In our system, aphid may have affected biotic interactions through three main non-excluding effects on *T. absoluta*: (i) parasitoid-mediated interactions, (ii) resource competition, and (iii) plant-mediated indirect interactions.

The aphid did provide food source (honeydew) benefiting to the parasitoid *N. tutae* (at least increasing its longevity), and so, a negative indirect interaction toward *T. absoluta* occurred through increased parasitoid-induced mortality in the leafminer. Therefore, such effect could be classified as apparent amensalism (–, 0) (Chailleux et al. 2014b) as there was no parasitoid-mediated obvious effect of *T. absoluta* toward the aphid (Fig. 5). Indeed, albeit *T. absoluta* larvae density was strongly reduced by parasitoid *N. tutae*, there was no change in the *M. euphorbiae* population growth; therefore, any positive effect of *N. tutae* on aphid population growth (e.g., preventing leaf being destroyed by *T. absoluta* and reducing the resource competition between the two pests) might have been nullified by the occurrence

of other effect(s) (e.g., intraspecific competition could be a main driver in aphid population dynamic, Dixon et al. 1993; Mooney et al. 2008; Mohammed et al. 2019).

Resource competition between the two herbivores showed unilateral effects, with mostly *T. absoluta* being affected by aphids. The production of *T. absoluta* larvae was higher in the first part of the experiment, suggesting that no resource competition from aphid was occurring toward the leafminer larvae. However, this increase could be attributed to the positive effect that honeydew had on *T. absoluta* adults (i.e., increased longevity); living longer they produced more larvae. By contrast, in the second part of the experiment (when most adults from the first released cohort had died) there were fewer *T. absoluta* larvae in the presence of the aphid, independently of parasitoid presence. Thus, negative effects may have occurred through resource competition between leafminer larvae and aphids, notably owing to pullulating aphids on the plants. Tomato leaves heavily infested by aphids may be unsuitable for the leafminer (e.g., food quality and/or availability is decreased, Villemereuil and Lopez-Sepulcre 2011; Barabas et al. 2016). In addition, potential physical impairment in *T. absoluta* larvae may result from aphid presence, i.e., a leafminer larvae outgoing from a leaf mine could not dig a new mine owing to overcrowding aphids on the leaf. By contrast to the impact of aphid on *T. absoluta* through resource competition, the lack of effect of the leafminer toward aphid is somehow surprising as *T. absoluta* is known to have a major impact on tomato plants (being a defoliator herbivore). For example, previous studies reported that *T. absoluta* negatively affected biological traits and population dynamic of the whitefly *Bemisia tabaci*, another major sap-feeder insect on tomato (Bompard et al. 2013; Jaworski et al. 2015; Dong et al. 2018). Such discording results may be linked to the mobility habits of the two pests (aphid and whitefly) which differ drastically and could have its importance in their survival when competing with a defoliating insect. Despite being both sap feeders, mobility of whiteflies is quite limited in non-imaginal stages: only the first nymph stage can move (and barely), the other nymph stages are totally immobile and they die if the hosting leaf is destroyed. By contrast, all aphid stages are well mobile and the destruction of leaves by *T. absoluta* larvae does not lead to aphid death; they can move and start feeding on another part of the plant. Finally, *T. absoluta* may simply not have reached densities able to negatively impact aphid population through resource competition in our present study.

Aphids can also be involved in plant-mediated indirect interactions (Stout et al. 2006; Mouttet et al. 2011; Moreira et al. 2018) through triggering salicylic acid-pathway and subsequent plant chemical defenses (Walling 2000). Through this mechanism, *M. euphorbiae* may have negatively affected leafminer population dynamic (by lowering down population growth rate). Multiple studies documented

that sap feeders could affect negatively the performance of leaf chewers (Zhang et al. 2005; Inbar and Gerling 2007; Soler et al. 2012; Mouttet et al. 2013) and our study is in concordance with these data. In addition, the lack of impact of *T. absoluta* on aphids also matched with results of a previous study from Mouttet et al. (2013) which demonstrated lack of plant-mediated effect of *T. absoluta* to another sap feeder (*B. tabaci*). Finally, because our experimental design did not separate spatially both herbivores on the plants, it was not possible to distinguish between direct and plant-mediated indirect interactions between *T. absoluta* and aphid, although both interactions are likely confounded in realistic conditions.

Implication in biological control

Under microcosm and laboratory conditions, the ectoparasitoid *N. tutae* has proved to be a potential biological control agent of *T. absoluta*, targeting the larvae stage (Chailloux et al. 2014a; Biondi et al. 2018; Dong et al. 2018). In the present study we demonstrated that *N. tutae* can provide effective biological control of *T. absoluta* in tomato greenhouse, keeping the population at relatively low densities during the course of the experiment. Alternative food sources (e.g., honeydew produced by aphid) can help keeping parasitoids close to crops, in addition to providing and impacting the performance and longevity of parasitoids (Wäckers et al. 2008; Benelli et al. 2017) and this without promoting pest population growth (despite positive effect on the adult stage of the pest). However, aphids are pests that are targeted also by pest management program(s) and controlling their populations may compromise any benefits associated with their presence in the framework of *N. tutae*-based biological control. Other research has been carried out to select plant flowers, as alternative food sources, facilitating the establishment of *N. tutae* parasitoids and to improve biological control of *T. absoluta* (Balzan and Wäckers 2013; Arnó et al. 2018). Other alternatives such as the use of banker plants has been subjected to great interest as a means of biological control of invasive and/or key pests (Bodino et al. 2018; Kruitwagen et al. 2018; Wang et al. 2018). Banker plant systems are based on the use of non-commercial plants infested with non-pest herbivores serving as alternative host-prey for predators or parasitoids (Frank 2010; Parolin et al. 2012; Li et al. 2015; Zhao et al. 2017; Jaworski et al. 2019). When such plant banker systems are infested by aphids (or more generally by sap feeders), they may serve as sources of alternative foods, notably honeydew. Studies determining the factors limiting or potentially optimizing the biological control through manipulating honeydew producers are still needed to develop further biological control and IPM programs.

Acknowledgements The authors thank the project ASCII (FP7 IRSES no. 318246) for funding to ND and MRC, the University of Catania (Project 2016–2018 “Emergent Pests and Pathogens and Relative Sustainable Strategies—5A722192113) and the Italian Ministry of Education, University and Research (MIUR) (PRIN project 2015 “BIOPIC” No. 2015BABFCF) for funding to AB and LZ, the project STomp (ARIMNET2 no. 618127) for funding to AB, AVL, LZ and ND, the IPM Innovation Lab (USAID Cooperative Agreement no. AID-OAA-L-15-00001) for funding to ND and MRC, and the EUCLID project (H2020-SFS-2014, no. 633999) for funding to PB, EAD and ND.

Author contributions statement ND and MRC designed the experiment. MRC, PB, EAD and YW performed the bioassays. ND, AVL, AB and LZ provided technical and material supports. LSM and MRC analyzed the data. MRC, LSM and ND led the writing of the manuscript and all authors read and approved the manuscript.

Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

Human and animal rights This article does not contain any studies with human participants or animals (others than insects) performed by any of the authors.

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