Biological Control 205 (2025) 105772

Contents lists available at ScienceDirect

Biological Control

journal homepage: www.elsevier.com/locate/ybcon

Compatibility of biocontrol agents with host plant resistance for management of the South American tomato pinworm *Phthorimaea absoluta*

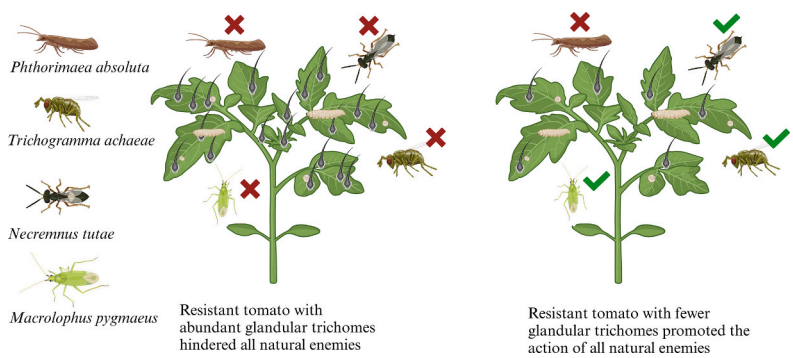
Ayomide Joseph Zannou [a], Judit Arnó [b], Jörg Romeis [a], Jana Collatz [a,*]

[a] Agroscope, Research Division Agroecology and Environment, Reckenholzstrasse 191, 8046 Zurich, Switzerland
[b] IRTA, Sustainable Plant Protection, 08348 Cabrils, Catalonia, Spain

HIGHLIGHTS

- We evaluated the effectiveness of three natural enemies on six tomato genotypes varying in resistance to *P. absoluta*.
- Resistant tomato *S. arcanum* presenting high glandular trichome densities impaired the performance of all natural enemies.
- Resistant domesticated tomato Corona F1 and resistant wild tomato *S. neorickii* supported all natural enemies.
- The findings provide important insights for integrated pest management (IPM) strategies against *P. absoluta*.

GRAPHICAL ABSTRACT



ARTICLE INFO

Keywords:
Host plant resistance
Predator
Parasitoid
Trichome density
Tri-trophic interactions
Integrated pest management

ABSTRACT

Integrating host plant resistance with biocontrol agents represents a promising strategy for sustainable management of *Phthorimaea* (*Tuta*) *absoluta* (Meyrick) (Lepidoptera: Gelechiidae), an invasive pest that poses a significant global threat to tomato production. However, morphological resistance traits, secondary metabolites, and plant volatiles in tomato may have adverse effects on natural enemies, thereby influencing the overall efficacy of pest control. This study evaluated the performance of three natural enemies across six tomato genotypes exhibiting various levels of resistance to *P. absoluta*. First, we evaluated the performance of the parasitoid *Trichogramma achaeae* on eggs, derived from moths reared on the different tomato genotypes, both in isolation and when presented on respective tomato leaflets. Second, we assessed the performance of the parasitoid *Necremnus tutae* on tomato genotypes that hosted *P. absoluta* larvae. And finally, we investigated the predatory capacity of the mirid *Macrolophus pygmaeus* on tomatoes hosting eggs and larvae of *P. absoluta*, all derived from moths reared on these genotypes, as well as the survival of predator nymphs on the different tomato genotypes, both with and without *P. absoluta* eggs. The *P. absoluta*-susceptible tomatoes, the resistant domesticated Corona F1 and the resistant wild tomato species *Solanum neorickii* had no significant impact on the parasitism and emergence rates of both parasitoids, or on the predatory efficacy and survival of predator nymphs. In contrast, the resistant wild *Solanum arcanum* negatively affected the performance of both parasitoids, reduced predatory efficacy and survival of first-instar nymphs, and increased the development time of predator nymphs. Our

* Corresponding author.
E-mail addresses: ayomide.zannou@agroscope.admin.ch (A.J. Zannou), judit.arno@irta.cat (J. Arnó), joerg.romeis@agroscope.admin.ch (J. Romeis), jana.collatz@agroscope.admin.ch (J. Collatz).

https://doi.org/10.1016/j.biocontrol.2025.105772
Received 6 February 2025; Received in revised form 10 April 2025; Accepted 17 April 2025
Available online 18 April 2025
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findings indicate that the resistant genotypes Corona F1 and *S. neorickii* appears to be compatible with all the natural enemies, whereas *S. arcanum* appears incompatible.

1. Introduction

Integrated Pest Management (IPM) is a holistic approach to pest management that integrates multiple strategies to minimize pest populations while reducing environmental impact and economic costs (Flint and van den Bosch, 1981). In particular, the significance of IPM lies in its capacity to decrease reliance on chemical pesticides, which can have adverse effects on human health, non-target organisms, and the environment (Colmenárez et al., 2016). By integrating multiple control tactics, IPM seeks to establish a sustainable and resilient agricultural system capable of withstanding long-term pest pressures (Gott and Coyle, 2019). When dealing with an invasive pest like the South American tomato pinworm *Phthorimaea absoluta* (formerly *Tuta absoluta*) (Meyrick) (Lepidoptera: Gelechiidae) (Chang and Metz, 2021), implementing IPM strategies that utilize alternative, eco-friendly control methods, such as biological control agents and host plant resistance, can be a promising approach (Bottega et al., 2017; Giorgini et al., 2019; Desneux et al., 2022). This moth is an economically important pest threatening tomato production worldwide (Desneux et al., 2010; Biondi et al., 2018; Chepchirchir et al., 2023).

Plant defense traits exert significant influence on both the numerical and functional responses of natural enemies mediated through semiochemicals, plant toxins, nutrients, and physical mechanisms (Peterson et al., 2016). To protect from herbivory, plants produce trichomes, volatiles, and secondary metabolites that affect natural enemies in various ways. Volatiles can attract natural enemies to the pest, thereby facilitating tri-trophic interactions (War et al., 2018; Bueno et al., 2019; Ayelo et al., 2021). Conversely, trichomes serve as physical barriers, mechanically and directly impeding natural enemies from accessing the pest (Bottega et al., 2017). Secondary metabolites, like glycoalkaloids, can directly harm natural enemies that feed on the plant, such as the zoophytophagous predators *Nesidiocoris tenuis* (Reuter) and *Macrolophus pygmaeus* (Rambur) (both Hemiptera: Miridae), thereby reducing their effectiveness (Erb et al., 2021). They may also indirectly impair the natural enemies by affecting the herbivore's digestion and development, thus resulting in lower host quality (Campbell and Duffey, 1979; Opitz and Müller, 2009; Erb et al., 2021). Additionally, some herbivorous larvae accumulate and sequester metabolites for self-defense, which can indirectly compromise the development and effectiveness of larval parasitoids and predators (Opitz and Müller, 2009; Erb et al., 2021). Furthermore, herbivorous adults that have developed on plants with secondary metabolites can transfer these compounds to their eggs, providing chemical defense against egg parasitoids and predators (Opitz and Müller, 2009).

Tomato plants exhibit a variety of morphological and chemicals traits that play critical roles in protecting them against herbivores (Vitta et al., 2016). Morphological traits include physical structures such as trichomes (hair-like appendages) on leaves and stems, which can act as both physical barriers and sites for the production of defensive chemicals. In tomato, trichomes are categorized into glandular types I, IV, VI, and VII; and non-glandular trichomes II, III, V and VIII (McDowell et al., 2011). Resistance to *P. absoluta* in tomato plants is associated with type and density of trichomes, volatile emission and secondary metabolite content (Salazar-Mendoza et al., 2023; Kumaraswamy et al., 2024; Zannou et al., 2024). Those factors may vary among cultivars and between cultivated and wild tomato (Zhang et al., 2020; Zannou et al., 2024). Tomato genotypes with enhanced resistance not only affect *P. absoluta* survival but also interact with parasitoids and predators, thereby influencing their performance (Romeis et al., 2005; Wangari Nderitu et al., 2020).

Among natural enemies, the egg parasitoid *Trichogramma achaeae* Nagaraja & Nagarkatti (Hymenoptera: Trichogrammatidae), the larval parasitoid *Necremnus tutae* (Ribes & Bernardo) (Hymenoptera: Eulophidae) and the mirid predator *M. pygmaeus* are three predominant species. *Trichogramma achaeae* is commercially available and already successfully used in inundative biological control programs against *P. absoluta* (Cherif et al., 2019; Mansour and Biondi, 2021). Further, *N. tutae* an ectoparasitoid of late instar larvae of *P. absoluta*, is naturally occurring in greenhouses in the Mediterranean region (Urbaneja et al., 2012), contributing to the control of the pest with parasitism rates up to 73 % and mortality via host feeding and host killing up to 92 % (Crisol-Martínez and van der Blom, 2019; Zhang et al., 2022; Gonthier et al., 2023; Koller et al., 2024). Finally, the mirid predator *M. pygmaeus*, which preys preferentially on *P. absoluta* eggs but can also consume first instar larvae (De Backer et al., 2014; Duarte Martinez et al., 2023), is commercialized and used widely in European greenhouses against *P. absoluta* (Ferracini et al., 2019).

In an integrated pest management approach, understanding the interactions between natural enemies of *P. absoluta* and host plant resistance remains a paramount step to achieve pest control (Han et al., 2019b). The combination of natural enemies with host plant resistance can potentially enhance control efficacy, however, negative interactions may also occur. Currently, our understanding of the interaction between tomato host plants and mirid predators against *P. absoluta* is limited to studies by Bottega et al. (2017), Bueno et al. (2019) and Guruswamy et al. (2023) which have primarily focused on morphological traits, particularly trichomes. Similarly, the intricate relationship between physical traits (such as trichomes) and chemical traits (especially secondary metabolites) on both egg and larval parasitoids of *P. absoluta*, as well as the effects of secondary metabolites on mirid predators, remains largely unexplored (Han et al., 2019b). In this context, we characterized the interaction between the natural enemies of *P. absoluta* and different tomato plants with various genotypes of either domesticated or wild origin and with diversified morphology and differences in resistance traits that were identified in a previous study (Zannou et al., 2024). We evaluated (1) the efficacy of *T. achaeae,* both in presence and absence of the plant, when parasitizing *P. absoluta* eggs derived from parents produced on different tomato genotypes, (2) the performance of *N. tutae* on larvae developing on different tomatoes genotypes; and (3) the development and predation rate of *M. pygmaeus* on different tomato genotypes.

2. Material and methods

2.1. Plant material

Six tomato genotypes including *Solanum arcanum*, *S. neorickii* and *S. lycopersicon* var. Corona F1 which exhibit resistance against *P. absoluta*, as well as *S. lycopersicon* var. Rentita, Noire de Crimée, and Romabelle, which are more susceptible to pest attacks were selected based on a previous study (Zannou et al., 2024). *Solanum arcanum* possesses the highest density of glandular trichomes, while the other genotypes predominantly feature non-glandular trichomes (Zannou et al., 2024). Wild tomatoes *S. arcanum* and *S. neorickii* were received from the UC Davis/CM Rick Tomato Genetic Resource Centre (TGRC), and the other varieties were obtained from commercial companies in Switzerland (Bigler Samen Sa and Samen Mauser). Prior to seeding, seeds of *S. arcanum* and *S. neorickii* were treated with a 3 % hypochlorite solution for 30 min, then rinsed under running water and sown immediately, following TGRC guidelines. Seedlings were grown in trays with organic substrate for one month before being transplanted into 10 cm pots filled with organic substrate enriched with long-term fertilizer (3

kg/m3, Manna Cote 4 M, Hauert Düngerwerke GmbH, Germany). Plants were grown in the greenhouse at 25 ± 5 °C and 60 ± 10 % RH, irrigated twice per week and held up by a string trellis secured to an overhead rope. No pesticides were applied. For experiments, plants were 4–6 weeks post-transplanting, while the Rentita variety at 4–8 weeks post-transplant was used for *P. absoluta*, *N. tutae* and *M. pygmaeus* rearing.

2.2. Insects

2.2.1. Phthorimaea absoluta

The *P. absoluta* colony was obtained from Andermatt Biocontrol (Grossdietwil, Switzerland) and reared in climate chambers at 25 ± 1 °C, 70 ± 10 % RH, and a 16:8h L:D photoperiod. Adult moths were maintained in a mesh cage (50 × 50 × 50 cm; bug dorm; MegaView Science Co. Ltd., Taiwan) containing cut tomato plants (var Rentita) and drops of honey provided on a Post-it® paper. The tomato plant stems were kept in a 1 L Erlenmeyer flask filled with water to preserve the plant freshness. After 72 h, infested plants were transferred to a new cage to initiate a new colony. Fresh tomato plants were provided for larval development until pupation.

Phthorimaea absoluta was reared on six tomato genotypes for one generation, and the eggs laid were used in experiments with *T. achaeae* and *M. pygmaeus*. For *N. tutae* assays, second-third instar larvae were used. One hundred adult moths from the culture (mixed sexes, 2–3-day-old) were released into each mesh cage (bug dorm, as described above), containing plants from one of the six genotypes. After 48 h, the adult moths were removed, and fresh plants of the respective genotypes were added until pupation occurred. To obtain second-third instar larvae, the infestation procedure described above was followed, with the larvae being maintained until they reached the desired developmental stages.

2.2.2. Trichogramma achaeae

Trichogramma achaeae was obtained from Bioline Agro-Sciences (France) and colonies of parasitoids were maintained on UV-irradiated eggs of *Ephestia kuehniella* Zeller (Lepidoptera: Pyralidae) from AGRO-LINE Bioprotect (Switzerland) in large acrylic glass tubes (10 cm diameter; 30 cm length). The tubes were covered with fine mesh on one side, whereas the other side was covered with a dark lid. UV-irradiated host eggs on a Post-it® paper were provided to the colonies alongside with honey-agar (water:agar:honey, 1 L: 8 g: 0.1 L) three times per week. Parasitized eggs were removed every 48 h and incubated in containers (5 cm diameter; 10 cm length). After about 10 days, newly emerged adults were transferred back into the rearing tube. The parasitoids were kept in climate chambers (22 ± 1 °C, 70 ± 10 % RH, 16:8h L:D) for at least 90 generations on *E. kuehniella* eggs prior to the experiments.

2.2.3. Necremnus tutae

A colony of *N. tutae* was established using individuals collected from commercial tomato fields in El Maresme county, Barcelona, Spain (Gonthier et al., 2024). Adults were maintained in mesh cages (bug dorm, see above) with honey droplets provided on Post-it® papers and tomato plants (var Rentita) infested with second and third instar larvae of *P. absoluta* offered as hosts for parasitism. Upon emergence, adult parasitoids were stored at 12 °C in plastic tubes (6.5 cm dia.; 8.5 cm length) with honey droplets for up to 10 days before being released (at a rate of 30 mixed sex adults) into new mesh cages containing larvae-infested plants to initiate a new colony. All female parasitoids used in the assays were less than one week old, naïve and mated (maintained with male for 2 days post-cooling). *Necremnus tutae* was kept in climate chambers at 25 ± 1 °C, 70 ± 10 % RH, and a 16:8h L:D photoperiod.

2.2.4. Macrolophus pygmaeus

Adult *M. pygmaeus* were obtained from Andermatt Biocontrol (Grossdietwil, Switzerland). To establish and maintain the predator stock colony, the individuals were confined in mesh cages (bug dorm, see above) on tomato plants (var Rentita). *Ephestia kuehniella* eggs were supplied *ad libitum* as a food source three times per week. The predators were kept in climate chambers (25 ± 1 °C, 70 ± 10 % RH, 16:8h L:D) for at least 4 generations prior to the experiments. All predators used in the experiments were either less than 3-days-old (females) or less than 1-day-old (nymphs). To obtain females, fifty adult predator couples were released into a separate cage containing two potted tomato plants (var Rentita) for oviposition and *E. kuehniella* eggs were provided as food *ad libitum*. One week later, tomato plants were removed and placed in an empty cage with a continued supply of *E. kuehniella* eggs until predators reached the adult stage. For first instar nymphs, a similar method was used; however, after isolating the plant in an empty cage, eggs were checked daily to collect freshly hatched nymphs.

2.3. Bioassays

All experiments were conducted in climate chambers at 25 ± 1 °C, 70 ± 10 % RH, and a 16:8h L:D photoperiod.

2.3.1. Effect of tomato genotype on Trichogramma achaeae

2.3.1.1. Volume of P. absoluta eggs. Tomato leaflets from the respective tomato genotypes, with their petioles inserted into agar solutions contained in plastic tubes (6.5 cm diameter; 8.5 cm length) covered with fine mesh (as described above) were used in the experiment. A single 3-day-old mated female from the first generation of *P. absoluta* was released in each tube and allowed to lay eggs for 4 h (n = 10 replicates). Thereafter, the moths were removed and 2 eggs per female (20 in total) were randomly selected for measurement. Egg length (L) and width (W) were measured using a digital stereo-microscope (Keyence VHX 6000) and the egg volume was calculated ($V = 4/3 \times \pi \times 1/2L \times 1/2W \times 1/2W$).

2.3.1.2. Eggs provided without tomato leaflets. To assess the indirect effect of tomato genotypes on *T. achaeae*, a fine mesh with eggs from the first generation (F1) of *P. absoluta* produced on the respective genotypes was offered to the parasitoids. To obtain these eggs, adult moths (F1) of mixed sexes (> 50; 2–3-day-old) were released into 1.3 L plastic jars covered with a fine mesh, and tomato leaves (from respective genotypes) were placed on top of the mesh to provide an odor source. Female moths were allowed to lay eggs on the underside of the mesh. After 24 h, the mesh was removed and sections of mesh with 20 eggs were carefully cut off. Thereafter, 20-egg-infested mesh section from each genotype were individually placed in plastic tubes (2 cm diameter; 6 cm length). One pair of naïve *T. achaeae* (2–5-day-old, naïve) was introduced into each tube for 24 h (n = 20–25 replicates). After this period, the parasitoids were removed to allow parasitized eggs to continue developing. Three days later, eggs that had turned black as observed under a stereomicroscope were considered as parasitized and kept in the same conditions until wasps emergence. Data on parasitism, offspring emergence and sex ratio were recorded at 10–15 days post parasitism.

2.3.1.3. Eggs provided on tomato leaflets. This experiment adhered to the previously described procedure, with the exception that tomato leaflets from the respective genotypes were utilized as oviposition sites instead of fine mesh. To obtain egg-infested leaflets, three leaves (each with three leaflets) with petioles placed in a 1 L Erlenmeyer flask filled with water were exposed to 50 adult *P. absoluta* (mixed sexes, 2–3-day-old) in a bug dorm cage (see above) for 24 h. Thereafter, leaflets were detached and the number of eggs was reduced to 20 by carefully removing excess eggs using a camel brush. The petiole of each 20-egg-infested-leaflet was inserted in a plastic tube (6.5 cm diameter; 8.5 cm length) containing an agar water solution (8 g: 1 L) to maintain hydration. The tubes were sealed with fine mesh. The agar solution was prepared 24 h prior to the experiment. One pair of *T. achaeae* (2–4-day-old, naïve) was released in each plastic tube for parasitization for 24 h (n = 21–25 replicates). After

this period, parasitoids were removed to allow parasitized eggs to continue developing until wasp emergence. Three days later, eggs that had turned black as observed under a stereomicroscope were considered as parasitized. Data on parasitism, offspring emergence and sex ratio were recorded at 10–15 days post parasitism.

2.3.2. Effect of tomato genotype on Necremnus tutae

To evaluate the performance of *N. tutae*, *P. absoluta* larvae were initially reared on respective tomato genotypes until they reached the second-third instar larvae (as described above). To obtain these larvae, tomato plants with 6 or 8 leaves from each genotype were exposed to 100 adult *P. absoluta* (mixed sexes, 2–3-day-old, from the rearing unit) in a bug dorm cage (see above) for infestation. After 48 h, the infested tomato plants were transferred into an empty cage for larval development until the third instar. Uninfested tomato plants of the same genotype were provided as needed. Afterwards, leaves from the middle part of an uninfested plant were artificially infested with twenty third instar larvae with a camel brush, and placed in 1.3 L plastic jars covered with a fine mesh. The leaf petiole of each leaf was sticking out of the jar through a hole at its basis. The petiole was diving into a container with water below the jar to keep the plant hydrated as described in Zannou et al. (2024). One pair of *N. tutae* (3-day-old, naïve and mated) was introduced into each plastic jar for 48 h (n = 22–23 replicates). Thereafter, parasitoids were removed, and at least 15 days later, emerged parasitoids, proportion of female offspring as well as emerged adult moths were recorded. The tibia length of all emerged parasitoids was measured under a stereomicroscope.

2.3.3. Effect of tomato genotype on Macrolophus pygmaeus

2.3.3.1. Female predation capacity. Leaflets from the different tomato genotypes infested with either *P. absoluta* eggs or larvae were offered to female predators. Eggs and larvae were obtained from the first generation of moths reared on the respective tomato genotypes as described above. To obtain egg-infested leaves, three leaves of the middle part of each tomato plant (each with three leaflets) were exposed to 50 adult moths (mixed sexes, 2–3-day-old) in a mesh cage for 24 h. Leaf petioles were inserted into 1 L Erlenmeyer flask and filled with water to keep the plants hydrated. After this period, leaflets were detached, and the number of eggs was adjusted to 100 after carefully removing excess eggs using a camel brush. For larvae infestation, 10 first-instar larvae were released on leaflets using a fine camel brush. First instar larvae were obtained by releasing adult moths (> 50, mixed sexes, 2–3-day-old) in 1.3 L plastic jars covered with a fine mesh, and tomato leaves (from respective genotypes) were placed on top of the mesh to provide an odor source. Female moths were allowed to lay eggs on the lower side of the mesh overnight (14–16 h). Larvae were collected approximately 96 h later. The quantity of eggs was determined by Duarte Martinez et al. (2023), which indicated that a single female *M. pygmaeus* can consume approx. 75 eggs within 24 h at 25 °C. The chosen number of larvae exceeded the reported maximum predation female *M. pygmaeus*, reaching up to 2.5 larvae within the same period and condition (Urbaneja et al., 2009). After infestation, both egg-infested and larva-infested leaflets were separately placed in plastic jars with their petioles inserted into an agar solution in plastic tubes (6.5 cm diameter; 8.5 cm length), and covered with fine mesh (as described above). A total of 21–24 jars were set per type of infestation and per tomato genotype. One 3-day-old single female *M. pygmaeus* was released into each plastic jar for 24 h. Prior to that, female predators were starved overnight (approx. 20 h) by being kept in 1.3 L plastic jars covered with a fine mesh, solely provided with cotton soaked in water. The numbers of preyed eggs and larvae were recorded using a stereomicroscope, thereby counting undamaged eggs and dead larvae. Additionally, the number of feeding marks on leaflets (Castañé et al., 2011) was also recorded.

2.3.3.2. Life-table parameters. *Phthorimaea absoluta* eggs derived from the first generation of moths reared on the different tomato genotypes and newly emerged first instar nymphs (≤ 24 h) were used. Leaves (with 5 or 7 leaflets) from the middle part of the tomato plants were infested with eggs as previously described, except that leaves were presented to 200 moths of mixed sexes to obtain leaflets containing approx. 150 eggs. Uninfested leaflets from the respective tomato genotype were used as control. Egg-infested leaflets and control leaflets of each genotype were separately placed in plastic jars with their petioles inserted into an agar solution in plastic tubes (6.5 cm diameter; 8.5 cm length) and covered with fine mesh (as described above). One single newly emerged nymph was released in each plastic jar (n = 21–24 replicates). Infested leaflets with approx. 150 eggs and uninfested leaflets were renewed every 48 h until nymphs molted into the adult stage. Nymphal survival and development time were recorded daily. The transition between nymphal stages was verified by the presence of molts.

2.4. Data analysis

Data were initially checked for normal distribution and variance homogeneity using the Shapiro-Wilk and Levene's test, respectively. Most data were not normally distributed, except for the volume of *P. absoluta* eggs. Thus, one-way ANOVA was used to analyze the differences in eggs sizes, followed by Tukey test ($P < 0.05$) for post-hoc mean separation.

A Generalized Linear Model (GLM) with a Poisson distribution with a logit link function was used to analyze the performance (number of parasitized eggs and emerged parasitoids) of *T. achaeae*. Tukey post-hoc test was carried out with the emmeans function for multiple comparisons across genotypes. The effect of egg size on the proportion of female offspring of *T. achaeae* was modelled using a binomial response variable with generalized linear models (GLM) and a logit link function. Dunn's post-hoc tests, with Bonferroni-Holm correction to adjust for multiple comparisons were used. Due to overdispersion, a model from the binomial family was chosen, which contained an additional estimate of a dispersion coefficient (also known as quasibinomial).

Due to the over-dispersed and excess of zeros in the data, and since the Akaike Information Criterion (AIC) for the Zero-Inflated Negative Binomial (ZINB) model was lower than that of the Negative Binomial model, indicating a better fit, the effect of tomato genotypes on the number of emerged *N. tutae* was modeled using the ZINB model. Tukey post-hoc test was carried out for multiple comparisons across genotypes. The proportion of offspring female of *N. tutae* across tomato genotypes was modelled using a binomial response variable with generalized linear models (GLM) and a logit link function. Due to overdispersion, a model from the binomial family was chosen, which contained an additional estimate of a dispersion coefficient. Kruskal-Wallis test was applied to compare differences in *N. tutae* adult tibia length. For both tests, multiple comparisons among the genotypes were performed using Dunn's post-hoc tests that employed a Bonferroni-Holm correction to adjust for multiple comparisons. A Generalized Linear Model (GLM) with a Poisson distribution with a logit link function was used to analyze the emergence of moths across tomato genotypes. Tukey post-hoc test ($P < 0.05$) was carried out with the emmeans function for multiple comparisons across genotypes.

The non-parametric Kruskal-Wallis test was used to assess how *M. pygmaeus* predation on various tomato genotypes influences the nymphal period of each instar and the overall duration of the nymphal period (the development time from the first instar to the adult stage). A Generalized Linear Model (GLM) with a Poisson distribution with a logit link function was used to analyze the effect of tomato genotype on the number of preyed eggs and larvae by female predators, as well as the number of feeding marks across tomato genotypes. Tukey post-hoc test was carried out for multiple comparisons across genotypes. Pearson's correlation coefficient was calculated to evaluate the relationship between egg/larvae predation and feeding marks on leaflets. Survival of

nymphal instars across tomato genotypes was analyzed using Kaplan–Meier survival curves and log-rank tests (Mantel–Haenszel test), followed by pairwise comparisons. All analyses were conducted using R software version 4.4.1 (R Core Team, 2024).

3. Results

3.1. Effect of tomato genotype on Trichogramma achaeae

3.1.1. Volume of Phthorimaea absoluta eggs

Eggs laid by moths reared on the different tomato genotypes showed significant differences in size (ANOVA, F = 11.57, df = 5, P < 0.001, Fig. 1). Moths reared on *S. arcanum* produced eggs that were significantly larger than those from Noire de Crimée, Rentita and Corona F1. Further, moths reared on *S. neorickii* and Romabelle F1 laid larger eggs compared to those reared on Noire de Crimée and Corona F1 (Fig. 1, Supplementary Table 1).

3.1.2. Eggs provided without tomato leaflets

In the absence of tomato plants, there was no significant difference in the number of parasitized eggs originating from *P. absoluta* that had developed on different genotypes (GLM, $X^2 = 3.5629$, df = 5, P > 0.05, Fig. 2a). Moreover, the number of emerged parasitoids did not differ significantly among eggs from *P. absoluta* from different tomato genotypes (GLM, $X^2 = 3.9484$, df = 5, P > 0.05, Fig. 2b). The proportion of female offspring emerging from eggs originating from *P. absoluta* that developed on Corona F1 was significantly lower than that from parents that developed on Romabelle F1 (GLM, P = 0.04, Fig. 2c), but not compared to eggs originating from parents that developed on any of the other genotypes (GLM, P > 0.05).

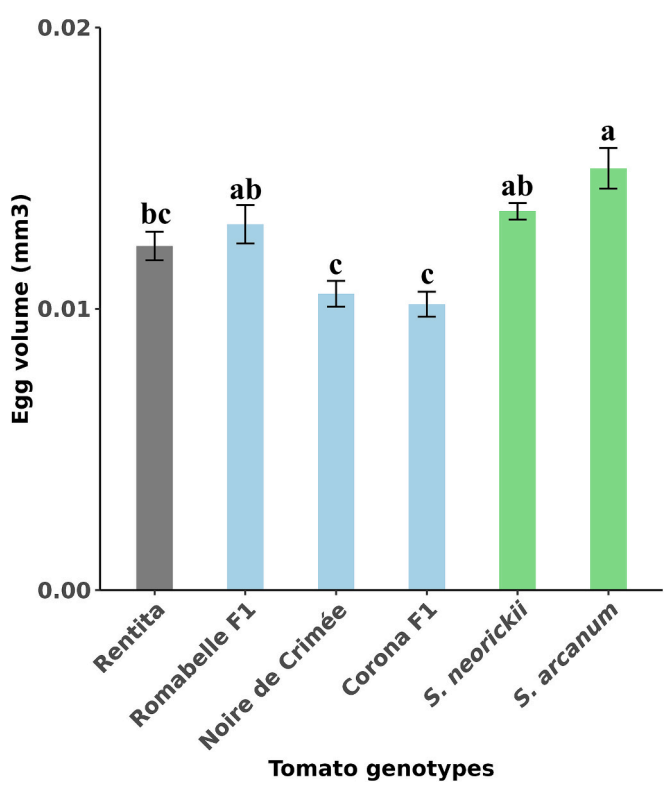

Fig. 1. Volume of *Phthorimaea absoluta* eggs (means ± SE) laid on leaflets of the different tomato genotypes by females reared on the same tomato genotypes. Different letters on the bar show significant differences (ANOVA, followed by Tukey's post hoc test, P < 0.001), n = 10.

3.1.3. Eggs provided on tomato leaflets

When eggs were presented on leaflets from the different tomato genotypes, this influenced significantly the number of parasitized eggs (GLM, $X^2 = 659.31$, df = 5, P < 0.001), with significantly fewer eggs parasitized on *S. arcanum* compared to the other tomato genotypes (Fig. 2d). There was no significant difference in number of parasitized eggs among the other genotypes. Further, no parasitoid offspring emerged from eggs laid on *S. arcanum*, while there were no significant differences in the number of emerged parasitoids (GLM, $X^2 = 1.2505$, df = 4, P > 0.05, Fig. 2e) or in the proportion of female offspring (GLM, $X^2 = 4.7868$, df = 4, P > 0.05, Fig. 2f) among the other genotypes.

3.2. Effect of tomato genotype on Necremnus tutae

The number of emerged parasitoids varied significantly among tomato genotypes ($X^2 = 25.234$, df = 5, P < 0.001, Zero-inflated negative binomial GLM, Fig. 3a), with significantly fewer emerged parasitoids on *S. arcanum* compared to those obtained on Noire de Crimée and *S. neorickii* (Fig. 3a). Likewise, the sex ratio differed significantly among tomato genotypes ($X^2 = 8.6119$, df = 4, P = 0.01, Binomial GLM, Fig. 3b). Female proportion on Corona F1 was significantly higher than on *S. neorickii* (GLM, P = 0.013). There was no significant difference in the sex ratio among Romabelle F1, Noire de Crimée and Rentita (Fig. 3b). Due to the low number of emerged parasitoids (0 male, 3 females), data from *S. arcanum* were excluded from the sex ratio and tibia length analysis. The tibia length of male and female offspring did not differ significantly among tomato genotypes (Kruskal-Wallis, male: $X^2 = 5.462$, df = 4, P > 0.05; female: $X^2 = 6.0071$, df = 5, P > 0.05, Fig. 3c). In accordance with the parasitism data (Fig. 3a), the number of emerged adult moths varied significantly among tomato genotypes (GLM, $X^2 = 212.39$, df = 5, P < 0.001, Fig. 3d), with significantly more adults emerging on *S. arcanum* compared to the other genotypes. The lowest numbers of emerged adult moths were obtained on Noire de Crimée and *S. neorickii*, those were significantly lower than on Romabelle F1 and Corona F1 (Fig. 3d).

3.3. Effect of tomato genotype on Macrolophus pygmaeus

3.3.1. Female predation capacity

3.3.1.1. Egg predation. Tomato genotype significantly influenced the number of eggs preyed by female *M. pygmaeus* (GLM, $X^2 = 1599.8$, df = 5, P < 0.001, Fig. 4a). Notably, the egg predation on *S. arcanum* was significantly lower compared to all other genotypes. The number of eggs preyed on Corona F1 was significantly lower than on *S. neorickii* and other domesticated tomato varieties. There were no significant differences in egg predation among *S. neorickii*, Rentita, Romabelle F1, and Noire de Crimée (Fig. 4a). Similarly, the number of feeding marks varied significantly among the tomato genotypes (GLM, $X^2 = 283.25$, df = 5, P < 0.001, Fig. 4b). Specifically, *S. arcanum* exhibited a significantly lower number of feeding marks than any of the other genotypes, while no significant differences were found among the other genotypes (Fig. 4b). Furthermore, no significant correlation was observed between eggs preyed and feeding marks on Corona F1 (r = 0.26, P = 0.25), Romabelle F1 (r = 0.34, P = 0.12), Noire de Crimée (r = 0.08, P = 0.73) and *S. neorickii* (r = 0.40, P = 0.069). In contrast, a significant positive correlation was found on Rentita (r = 0.43, P = 0.041) and *S. arcanum* (r = 0.53, P = 0.0081).

3.3.1.2. Larval predation. There was a significant difference in larval predation by female predators among the different tomato genotypes (GLM, $X^2 = 18.529$, df = 5, P < 0.01, Fig. 4c). The number of preyed larvae was significantly higher on *S. neorickii* compared to *S. arcanum* (Fig. 4c), but not when compared to the other genotypes. Likewise, the number of feeding marks differed significantly among tomato genotypes

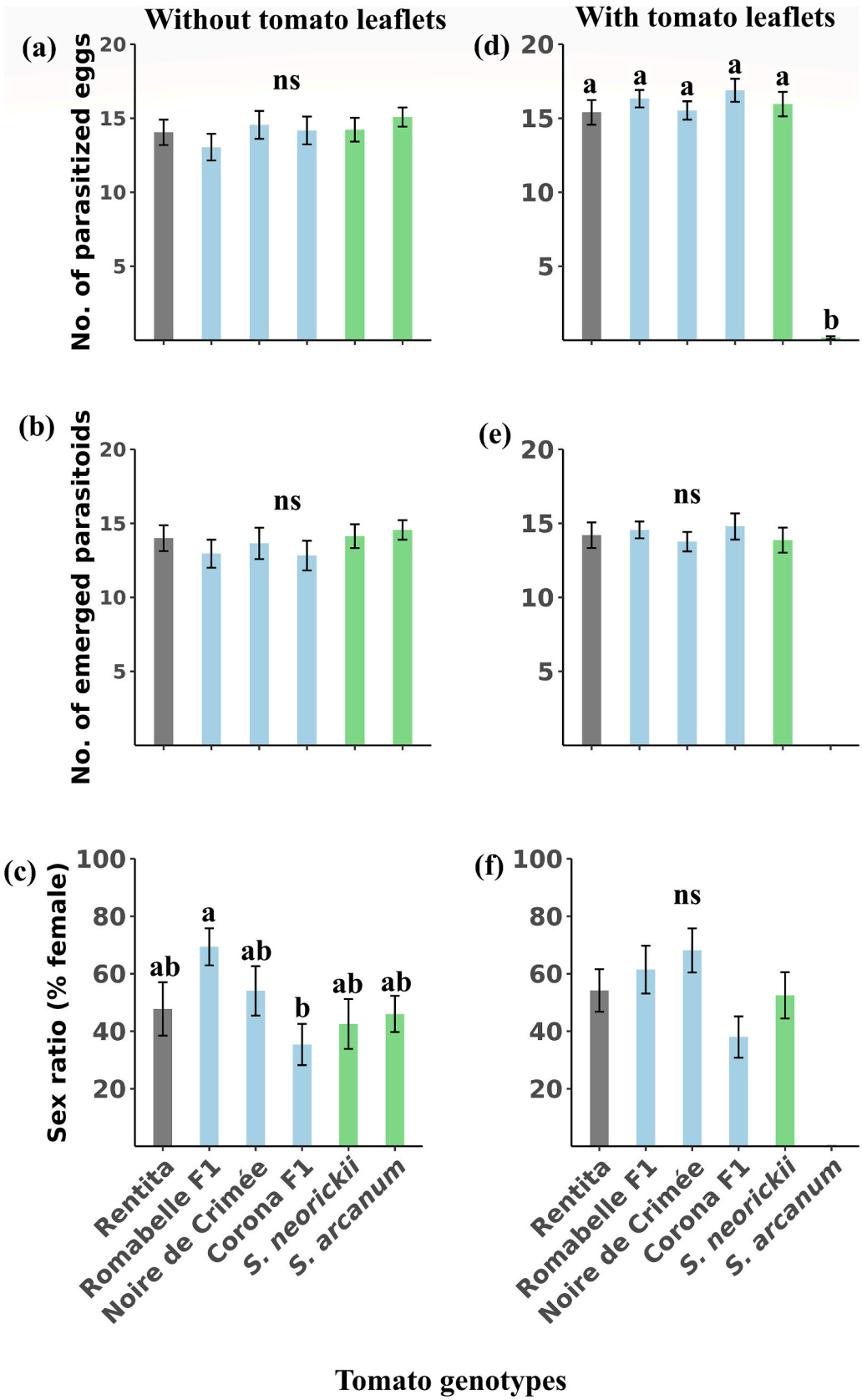

Fig. 2. Performance of *Trichogramma achaeae* on eggs produced by moths reared on different tomato genotypes. (**a-c**) in the absence of host leaflets: (**a**) Number of parasitized eggs, (**b**) Number of emerged parasitoids, (**c**) Proportion of emerged females; (**d-f**) in the presence of host leaflets: (**d**) Number of parasitized eggs, (**e**) Number of emerged parasitoids, (**f**) Proportion of emerged females. Means (±SE) with different letters are significantly different (**a, b, e**: GLMs with Poisson distribution and log link function, $P > 0.05$; **c**: GLM with quasibinomial distribution and log link function, followed by Dunn Test $P < 0.05$; **d**: GLM with Poisson distribution and log link function $P < 0.001$, followed by Tukey's post hoc test; **f**: GLM with quasibinomial distribution and log link function, $P > 0.05$), n = 20–25.

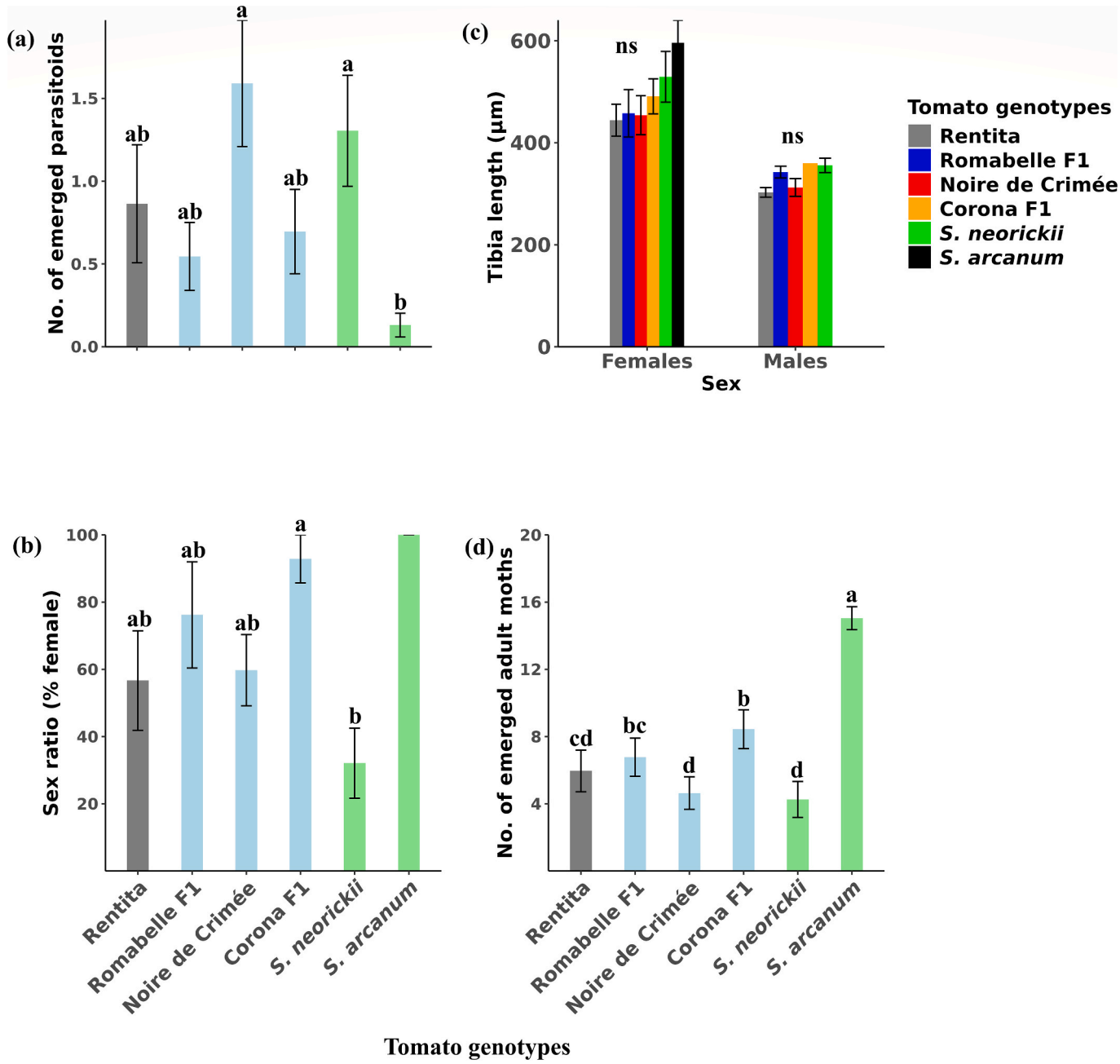

Fig. 3. Performance of *Necremnus tutae* on *Phthorimaea absoluta* larvae mining in leaflets from different tomato genotypes. (**a**) Number of emerged parasitoids, (**b**) Proportion of emerged females, (**c**) Tibia length of offspring, (**d**) Number of emerged adult moths. Means (±SE) with different letters are significantly different (**a**: Zero-inflated negative binomial GLM $P < 0.001$, followed by Tukey's post hoc test; (**b**) GLM with quasibinomial distribution and log link function $P = 0.01$, followed by Dunn Test; (**c**): Kruskal-Wallis test, $P > 0.05$; (**d**): GLM with Poisson distribution and log link function $P < 0.001$, followed by Tukey's post hoc test), n = 22–23.

(GLM, $X^2 = 89.075$, df = 5, $P < 0.001$), with *S. arcanum* exhibiting significantly fewer feeding marks than all other genotypes. In contrast, Corona F1 had a significantly higher number of feeding marks compared to Rentita and *S. neorickii*, while showing similar numbers compared to Noire de Crimée and Romabelle F1 (Fig. 4d). There was no significant correlation between the number of preyed larvae and the number of feeding marks on Romabelle F1 (r = 0.022, P = 0.93), Rentita (r = -0.0014, p = 1), Corona F1 (r = 0.14; P = 0.57), *S. arcanum* (r = 0.15, P = 0.52) and *S. neorickii* (r = -0.12, P = 0.6). In contrast, a significant negative correlation was found on Noire de Crimée (r = -0.47, P = 0.039).

3.3.2. Life-table parameters

The nymphal developmental time and survival of *M. pygmaeus* nymphs depended very much on whether tomato genotypes were offered with *P. absoluta* eggs or not (Fig. 5; Table 1).

When *P. absoluta* eggs were available, the survival of first-instar nymphs was significantly lower on *S. arcanum* compared to the other tomato genotypes (log-rank test, $X^2 = 24.9$, df = 5, $P < 0.001$, Fig. 5). In contrary, the survival rates of the other nymphal instars were similar across all tomato genotypes. When tomato leaflets were offered without *P. absoluta* eggs, the survival of the first-instar varied across genotypes (log-rank test, $X^2 = 21.8$, df = 5, $P < 0.001$, Fig. 5), being lower on *S. arcanum* compared to *S. neorickii*, Noire de Crimée and Romabelle F1. In contrast, no significant differences in the survival of the first-instar

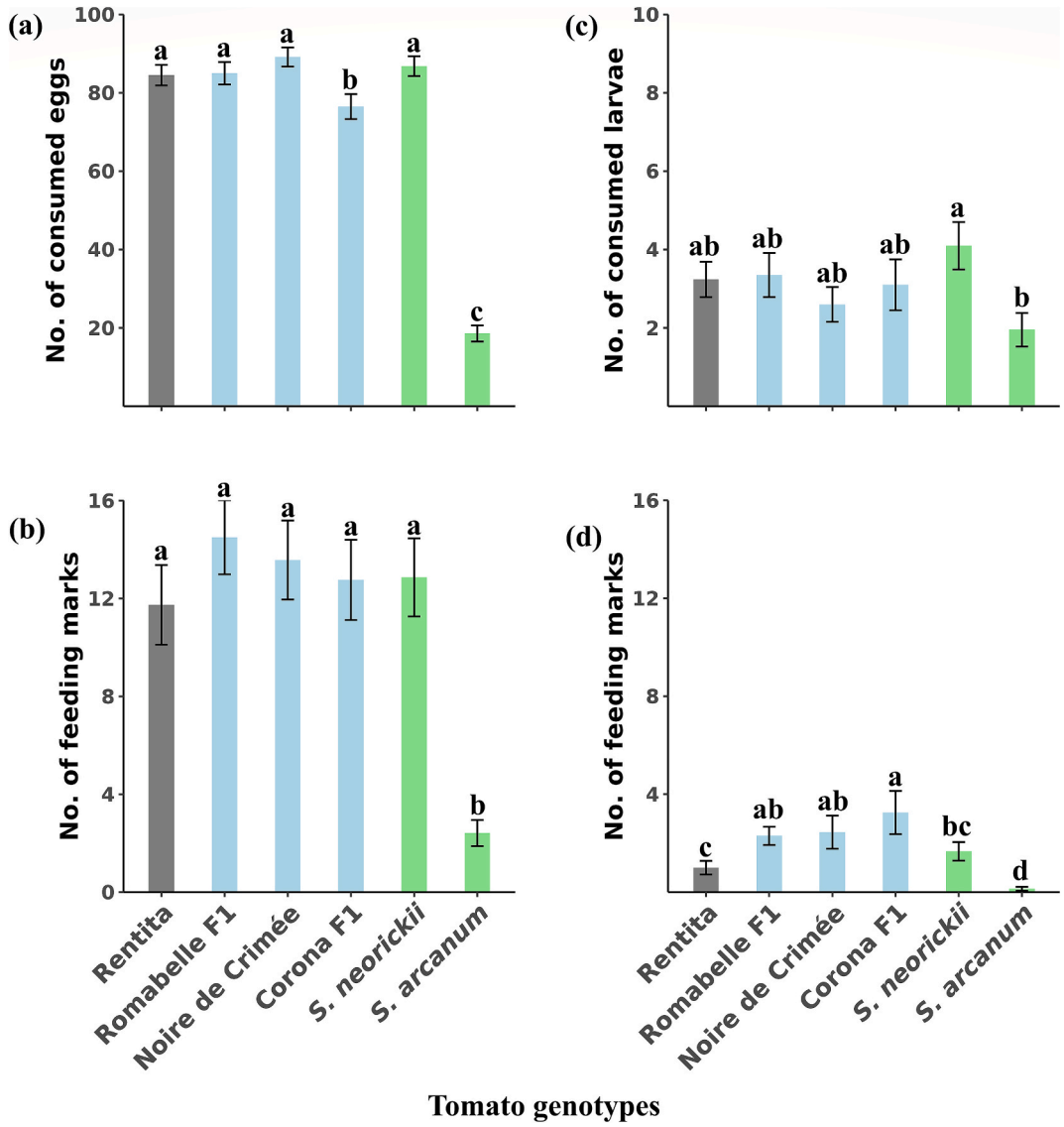

Fig. 4. Performance of female *Macrolophus pygmaeus* on different tomato genotypes when offered *Phthorimaea absoluta* eggs (**a, b**) or larvae (**c, d**). (**a**) Number of *P. absoluta* eggs consumed; (**b**) Number of necrotic rings inflicted; (**c**) Number of *P. absoluta* first-instar larvae consumed; (**d**) Number of necrotic rings inflicted. In all cases, observation period was 24 h. Means (±SE) with different letters are significantly different (**a, b, c, d** GLMs with Poisson distribution and log link function $P < 0.001$, followed by Tukey's post hoc test), n = 20–24.

nymphs among the other genotypes (log-rank test, $P > 0.05$, Fig. 5). Additionally, the survival rate of second-instar nymphs was significantly higher on *S. neorickii* compared to Rentita (log-rank test, $P < 0.01$ Fig. 5). Further, none of *M. pygmaeus* nymphs reached adulthood on any of the tomato genotypes, yet the highest number of first nymphal-instars completing this developmental stage was observed on Noire de Crimée, followed by *S. neorickii* (Supplementary Table 2). In the second instar, nymphs on *S. neorickii* achieved the highest completion rate (Supplementary Table 2). None of the nymphs completed any nymphal stage on *S. arcanum* (Supplementary Table 2). In contrast, no significant differences in the duration of the first-instar nymphal period were observed between the other genotypes (Supplementary Table 3).

Furthermore, when tomato leaflets carried eggs laid by *P. absoluta* reared on the same genotypes, the proportion of *M. pygmaeus* nymphs reaching adulthood was significantly influenced by tomato genotype (GLM, $X^2 = 10.655$, df = 5, $P = 0.03$; Table 1). This proportion was significantly lower on *S. arcanum* compared to Rentita, but not significantly different from the other genotypes (GLM, $X^2 = 2.8049$, df = 4, $P = 0.61$). The total nymphal development (from first instar nymph to adult) was significantly longer when nymphs developed on *S. arcanum* compared to the other tomato genotypes ($X^2 = 29.833$, df = 5, $P < 0.001$, Table 1). While there were no significant differences in first-, third- and fifth-instar nymphal periods, the development time on *S. arcanum* was significantly prolonged compared to Noire de Crimée in second-instar nymphs ($X^2 = 11.172$, df = 5, $P < 0.05$) and compared to Romabelle F1 and Noire de Crimée in the fourth-instar ($X^2 = 18.293$, df = 5, $P < 0.01$). Weight of the emerging *M. pygmaeus* adults did not differ among tomato genotypes (Table 1).

4. Discussion

This study is the first to assess the effect of tomato genotypes with varying levels of resistance to *P. absoluta* on three natural enemies, targeting distinct developmental stages of this pest; the egg parasitoid *T. achaeae*, the larval parasitoid *N. tutae* and the mirid predator *M. pygmaeus* which preys on both eggs and larvae. We found that the performance of natural enemies was unaffected by the resistant domesticated tomato Corona F1 and the resistant wild tomato

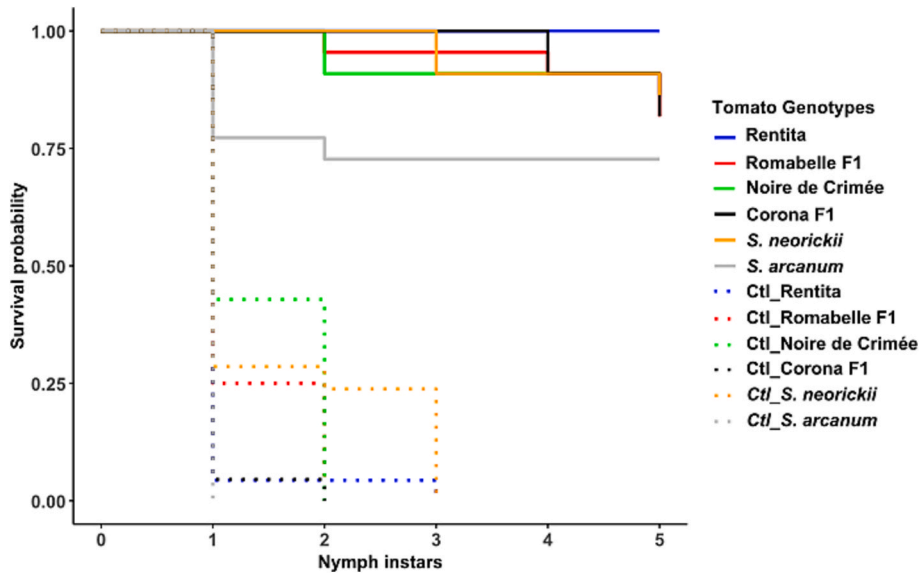

Fig. 5. Kaplan–Meier survival curves of *Macrolophus pygmaeus* nymphs developing on tomato leaflets with (solid lines) and without (dotted lines) *Phthorimaea absoluta* eggs. Significant differences among tomato genotypes are indicated **P < 0.05, ***P < 0.001 (log-rank test: Mantel–Haenszel, followed by pairwise comparison); ns, non-significant.; N1-N5: first- to fifth-instar nymph, n = 20–23.

Table 1
Nymphal developmental period, percent of nymphs reaching adulthood and adult weight of *Macrolophus pygmaeus* exposed to egg-infested leaflets from different tomato genotypes, with eggs derived from parents reared on the same genotypes (n = 22–23). All data are presented as mean ± SE (number of individuals), except for nymphs reaching adulthood, which is presented as percentage. N1-N5: first- to fifth-instar nymph.

Genotypes	Nymph instar developmental period (days)					Nymphal period (days)	Nymphs reaching adulthood (%)	Adult weight (mg)	
	N1	N2	N3	N4	N5			F	M
Romabelle F1	2.7 ± 0.5 (22)	2.4 ± 0.7 ab (21)	2.6 ± 1.5 (21)	2.4 ± 0.7b (20)	3.9 ± 0.2 (18)	13.7 ± 0.8 b (18)	81.8 ab	1.1 ± 0.1 (7)	0.7 ± 0.1 (11)
Noire de Crimée	2.5 ± 0.6 (22)	2.2 ± 0.6 b (20)	2.2 ± 0.6 (20)	2.3 ± 0.5b (20)	4.1 ± 0.7 (20)	13.4 ± 0.8 b (20)	90.9 ab	1.1 ± 0.1 (13)	0.7 ± 0.0 (7)
Rentita	2.7 ± 0.5 (23)	2.3 ± 0.6 ab (23)	2.1 ± 0.5 (23)	2.5 ± 0.6 ab (23)	3.9 ± 0.7 (23)	13.6 ± 0.7 b (23)	100 a	1.2 ± 0.1 (10)	0.7 ± 0.1 (13)
Corona F1	2.8 ± 0.5 (22)	2.4 ± 0.7 ab (22)	2.4 ± 0.5 (22)	2.5 ± 0.6 ab (20)	3.8 ± 0.4 (18)	13.6 ± 0.8 b (18)	81.8 ab	1.1 ± 0.1 (7)	0.7 ± 0.1 (11)
S. neorickii	2.7 ± 0.6 (22)	2.5 ± 0.9 ab (22)	2.4 ± 0.8 (20)	2.9 ± 0.7 ab (20)	3.8 ± 0.5 (19)	13.9 ± 0.9 b (19)	86.3 ab	1.1 ± 0.2 (11)	0.7 ± 0.1 (8)
S. arcanum	3.2 ± 1.2 (17)	2.9 ± 0.8 a (16)	2.2 ± 0.7 (16)	3.0 ± 0.6 a (16)	4.1 ± 0.6 (16)	15.5 ± 1.5 a (16)	72.7 b	1.0 ± 0.1 (9)	0.7 ± 0.1 (7)
Statistics	ns	*	ns	**	ns	***	*	ns	ns

Note: Statistical comparison among values within a column: Kruskal-Wallis test, * P< 0.05, ** P< 0.01, ***P< 0.001, ns: non-significant; multiple comparisons by Dunn Test: means followed by different letters within a column are significantly different (Nymphal instars developmental period, total nymphal period and adult weight); Nymphs reaching adulthood: GLM with quasibinomial distribution and log link function, followed by Dunn Test P< 0.05).

S. neorickii but was hampered by the resistant wild tomato *S. arcanum*.

Our results showed that in the absence of tomato leaflets, neither parasitism rates nor emergence success of *T. achaeae* differed between eggs laid by mothers reared on resistant or susceptible tomato genotypes. This is consistent with previous research where *Manduca sexta* (L.) (Lepidoptera: Spingidae) eggs laid by parents reared on diets with metabolites from resistant tomato did not affect parasitism rates of *Telenomus sphingis* Ashmead (Hymenoptera: Scelionidae) (Farrar and Kennedy, 1991). However, a lower proportion of female offspring emerged from eggs laid by parents reared on the resistant tomato variety, Corona F1, compared to those reared on the susceptible Romabelle F1. We assume that this effect may be attributed to difference in egg sizes, with smaller eggs produced by parents reared on Corona F1 and larger eggs by those reared on Romabelle F1. This suggests that while egg size may not impact immediate parasitism or developmental success, it influenced the decision of female *T. achaeae* to lay female eggs as has been reported for various *Trichogramma* species (King, 1987; Bourchier et al., 1993; Kishani Farahani et al., 2016; Moghaddassi et al., 2019). Further, moths reared on resistant plants may accumulate chemical compounds, such as secondary metabolites, which can be transferred to their eggs, potentially reducing egg nutritional quality or enhancing defense mechanisms, thereby affecting egg quality (Gols and Harvey, 2009; Opitz and Müller, 2009). The observation of similar proportions of female offspring emerging from larger eggs laid by parents reared on resistant genotypes, such as *S. arcanum* and *S. neorickii*, and on the susceptible Romabelle F1 offers two possible interpretations. Either defense compounds were transferred from parents to the eggs without affecting parasitoid development and sex allocation, or no such compounds were transferred. Further research is required to elucidate maternal effects on the potential transfer and dynamics of defense compounds in progeny of *P. absoluta*.

Nevertheless, in the presence of tomato leaflets, the resistant wild genotype *S. arcanum* markedly impacted the performance of both *T. achaeae* and *N. tutae* as well as the predatory performance and nymphal survival of *M. pygmaeus*. *Solanum arcanum* possesses abundant glandular trichomes types I and IV (Zannou et al., 2024), which likely

prevented *T. achaeae* from effectively parasitizing *P. absoluta* eggs, since no parasitoid offspring emerged. The dense glandular trichomes on *S. arcanum* appear to impede parasitoid movement and foraging behavior through physical entrapment. These findings align with other studies that show the negative effect of glandular trichomes on minute wasps. For instance, *T. pretiosum* and *T. sphingis* were entrapped by tomato glandular trichome exudates, thereby reducing their foraging behavior and efficacy against *Helicoverpa zea* (Boddie) (Lepidoptera: Noctuidae) and *M. sexta* (Kennedy et al., 1994; Gonçalves-Gervàsio et al., 2000; Kennedy, 2003). Additionally, pigeon pea plants with longer trichomes physically blocked *T. chilonis* from successfully parasitizing eggs of *Helicoverpa armigera* (Hübner) (Lepidoptera: Noctuidae) (Romeis et al., 1998). Therefore, a higher density of glandular trichomes especially types I and IV constitutes a handicap for the effectiveness of *T. achaeae* against *P. absoluta*. Further, *S. arcanum* prevented parasitism of *P. absoluta* larvae by *N. tutae*. This indicates that even relatively large parasitoids suffer on tomato genotypes with abundant glandular trichomes. Similar results were obtained by Kennedy et al. (1994), who reported that the efficacy of *Campoletis sonorensis* (Cameron) (Hymenoptera: Ichneumonidae) and *Cotesia congregata* (Say) (Hymenoptera: Braconidae), two larval parasitoids of *H. zea*, was reduced on resistant tomatoes presenting higher density of type VI glandular trichomes compared to susceptible tomatoes. Likewise, the larval parasitoid *Diadegma pulchripes* (Kokujev) (Hymenoptera: Ichneumonidae) failed to parasitize *Phthorimaea operculella* (Zeller) (Lepidoptera: Gelechiidae) larvae feeding on tomato leaves with higher levels of glandular type VI (Mulatu et al., 2006). In a previous study, there was 20 % mortality of *P. absoluta* on *S. arcanum*, whereas mortality on the other genotypes was either similar or lower than that of *S. arcanum* (Zannou et al. 2024). Thus, the high number of emerged adult *P. absoluta* on *S. arcanum* compared to other genotypes indicates that *N. tutae* was also unable to achieve host killing or host feeding. In addition, larvae feeding on resistant plants might sequester secondary metabolites as defensive compounds, which could reduce their nutritional suitability or even deter parasitism (Opitz and Müller, 2009; Erb et al., 2021). For instance, Ghosh et al. (2023) reported that the performance of the larval parasitoid *Cotesia glomerata* (L) (Hymenoptera-Braconidae) was negatively affected on larvae fed high-glucosinolate plants compared to those fed low-glucosinolate plants. Therefore, in addition to glandular trichomes, the quality of *S. arcanum*-feeding larvae may have also played a role in *N. tutae* failure, yet we were not able to address the direct effect of larvae on the parasitoid, as *N. tutae* does not parasitize host larvae outside their mine (Zhang et al., 2022; Gonthier et al., 2023).

We also found that *S. arcanum* reduced predatory effectiveness on both eggs and larvae, as well as feeding marks caused by *M. pygmaeus*. This tomato species also extended the nymphal development period and reduced the survival rate of first-instar predator nymphs. These results underscore the inhibitory effect of dense glandular trichomes, which create a hostile environment for predators by hindering prey access and the impeding their development. Similarly, Bottega et al. (2017) reported that higher numbers of type I and IV glandular trichomes impaired the prey consumption and foraging behavior of *Podisus nigrispinus* (Dallas) (Heteroptera: Pentatomidae) feeding on *P. absoluta* larvae, leading to reduced survival and extended development time on resistant tomatoes compared to a susceptible cultivar. Likewise, these trichomes were shown to prolong both early and late instar periods, as well as the overall development period, leading to increased mortality of nymphs and adults of the flower bug *Orius laevigatus* (Fieber) (Hemiptera: Anthocoridae) on *P. absoluta* (Guruswamy et al., 2023). Moreover, the predation rate of the tobacco hornworm *M. sexta* by *Podisus maculiventris* (Say) (Hemiptera: Pentatomidae) was reduced by 66 % on highly resistant tomato compared to less resistant tomato (Kaplan and Thaler, 2010). Therefore, while *M. pygmaeus*, as a larger predator, may exhibit greater tolerance to trichomes than small parasitoids like *T. achaeae* (Bueno et al., 2019), the physical obstruction from dense trichomes on *S. arcanum* still reduced its prey capture success, prolonged development time, and increased mortality, particularly in first-instar nymphs.

While *S. arcanum* affected all three natural enemies in our study, both the resistant *S. neorickii* and Corona F1 tomatoes, which possess fewer glandular trichomes and greater numbers of non-glandular trichomes, did not adversely affect the performance of either parasitoids or *M. pygmaeus*. Similar results were observed by Bueno et al. (2019), when differences in trichome density between resistant and susceptible tomatoes did not deter the efficacy of three predators *Campyloneuropsis infumatus* (Carvalho), *Engytatus varians* (Cyrova) and *Macrolophus basicornis* (Stal) (Hemiptera: Miridae). The authors argue that these predators are likely specialists in dealing with glandular trichomes. Moreover, Kennedy et al. (1994) reported that resistant tomato genotypes with higher numbers of type VI glandular trichomes did not impair the parasitism rates of *Cotesia marginiventris* (Cresson) and *Cardiochiles nigriceps* Viereck (both Hymenoptera: Braconidae) on *H. zea* larvae. In contrast, a domesticated tomato with abundant glandular trichomes reduced *T. pretiosum* searching efficiency and effectiveness against *P. absoluta* (Ghorbani et al., 2019). Thus, we assume that the components of the glandular trichomes of the resistant tomatoes (*S. neorickii* and Corona F1) provide no significant barrier, allowing *T. achaeae*, *N. tutae* and *M. pygmaeus* to move across the leaf surface and locate *P. absoluta* eggs and larvae. Further, the lack of chemical deterrents from non-glandular trichomes also supports better predatory and parasitoid performance (Mitchell et al., 2016). Furthermore, the parasitism of *N. tutae* on larvae fed on the two other resistant genotypes *S. neorickii* and Corona F1 remained unaffected compared to susceptible tomatoes. While we could not find any clear indication of plant chemistry affecting the natural enemies via transmission to their hosts or prey, defense compounds that are transferred to hosts may even be beneficial for natural enemies (Bowers, 2009; Gols and Harvey, 2009). For instance, *C. glomerata* grew larger when developing on larvae fed plants with higher glucosinolate levels compared to those fed plants lower in these secondary compounds (Harvey et al., 2003). In contrast, *P. operculella* larvae that developed on a resistant tomato, when offered directly to *D. pulchripes*, showed no impact on parasitism rates, offspring, or adult fitness (Mulatu et al., 2006).

The differential effects of glandular trichomes on the performance of both parasitoids and predators underscore the importance of understanding plant traits within the framework of biological control strategies. While resistant plants like *S. arcanum* may reduce herbivore populations, they can also inadvertently limit the effectiveness of natural enemies by creating physical and chemical barriers to parasitism and predation. This trade-off poses a challenge for integrated pest management programs, which aim to optimize the use of resistant plants while supporting the activity of biocontrol agents (Han et al., 2019a; Desneux et al., 2022). To maximize the effectiveness of biological control against *P. absoluta*, it is essential to select tomato genotypes that exhibit moderate or high resistance, but do not possess high densities of glandular trichomes that interfere with natural enemy performance (Bueno et al., 2019). For instance, the prolonged *P. absoluta* larval period observed on the resistant genotypes *S. neorickii* and Corona F1 (Zannou et al., 2024) may increase the susceptibility of the larvae to parasitoids like *N. tutae,* thereby enhancing pest control, as predicted by the slow-growth, high-mortality hypothesis (Feeny, 1976; Benrey and Denno, 1997). Additionally, the release of natural enemies, such as *Trichogramma* species or Mirid predators into tomato crops carrying low densities of glandular trichomes could optimize their impact on pest populations (Romeis et al., 2005; Hagenbucher et al., 2013; Messelink et al., 2014; Pocius and Kersch-Becker, 2024).

5. Conclusion

In summary, the assessment of tomato genotypes with varying levels of resistance to *P. absoluta* on three key biocontrol agents revealed the critical role of glandular trichomes in the success of integrated pest

management strategies that combine host plant resistance with biocontrol agents. We found that tomato plants with high glandular trichome densities negatively impacted the performance of the biocontrol agents. This study demonstrates the importance of understanding the impact of plant traits on the performance of biocontrol agents against *P. absoluta*. To expand on these findings, further research into the transfer of specific secondary metabolites from resistant tomatoes to *P. absoluta* eggs and larvae, as well as their impact on natural enemies could provide insights into plant-pest-natural enemy interactions. This will enhance our understanding of the compounds involved in maternal effects at both the pest and natural enemy levels, ensuring compatibility with biocontrol agents and promoting sustainable pest management programs.

CRediT authorship contribution statement

Ayomide Joseph Zannou: Writing – original draft, Visualization, Validation, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Judit Arnó:** Writing – review & editing. **Jörg Romeis:** Writing – review & editing, Supervision, Methodology, Funding acquisition, Conceptualization. **Jana Collatz:** Writing – review & editing, Supervision, Project administration, Methodology, Funding acquisition, Conceptualization.

Declaration of Generative AI and AI-assisted technologies in the writing process

During the preparation of this work the authors used ChatGPT in order to improve the readability of the manuscript. After using this tool, the authors reviewed and edited the content as needed and take full responsibility for the content of the publication.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgements

We would like to thank Meng Zhang, Yueyao Zhang and Mario Waldburger for their excellent technical assistance. This research was supported by Agroscope, Switzerland. The first author was funded by the Swiss Government Excellence Scholarship Program. JA received funding from the Horizon Europe, European Union programme under Grant Agreement No 101060430 and from the CERCA Program of the Generalitat de Catalunya, Spain.

Appendix A. Supplementary material

Supplementary data to this article can be found online at https://doi.org/10.1016/j.biocontrol.2025.105772.

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