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Lobularia maritima as a nutrient-rich floral food source for two parasitoid wasps of *Tuta absoluta*

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With 3 figures

Abstract: *Tuta absoluta* (Meyrick) (Lepidoptera: Gelechiidae) is one of the main pests threatening tomato production worldwide. Since its detection in the Mediterranean basin, it has been the target of research aiming to reduce damage in tomato crops. Current conservation biological control approaches focus on the polyphagous predators *Macrolophus pygmaeus* (Rambur) and *Nesidiocoris tenuis* (Reuter) (Hemiptera: Miridae), which are very effective predators of the pest's eggs but have little effect on *T. absoluta* larvae. Surveys conducted in northeast of Spain have concluded that the eulophid *Necremnus tutae* Ribes & Bernardo and the braconid *Dolichogenidea gelechiidivoris* (Marsh) are the most abundant larval parasitoids. It is well known that adding floral resources near crops can provide high-quality food for natural enemies and thus enhance biological control. Previous studies showed that *Lobularia maritima* L. (Brassicaceae) flowers are a reliable food source for *N. tutae*. The present study examines whether the availability of *L. maritima* flowers positively influences the fitness of *D. gelechiidivoris* and the biological control of *T. absoluta* by parasitoids. To study this aspect, the performance of both wasps was evaluated in a simple and complex arena at high and low densities of *T. absoluta*, respectively. Our results demonstrate that the nectar of *L. maritima* is a nutrient-rich food source for both *N. tutae* and *D. gelechiidivoris* with profound implications on the biological control of *T. absoluta* in tomatoes.

Keywords: *Necremnus tutae*; *Dolichogenidea gelechiidivoris*; South American tomato pinworm; nectar; nutritional ecology; conservation biological control

1 Introduction

Invasive species have enormous ecological impacts on natural systems and directly affect integrated pest management (IPM) programs (Ragsdale et al. 2011; Fortuna et al. 2022). The South American tomato pinworm *Tuta absoluta* (Meyrick) (Lepidoptera: Gelechiidae) is one of the primary invasive pests threatening tomato (*Solanum lycopersicon* L.) production worldwide (Desneux et al. 2010; Biondi et al. 2018). Originating in South America, its impact extends beyond, invading regions in Europe, Africa, Asia, and Central America (Biondi et al. 2018; Han et al. 2019; Mansour et al. 2018; Verheggen & Fontus 2019). Since its first detection in the Mediterranean basin (Spain) in 2006, it has been the target of intensive research aiming to reduce its negative impact on tomato crops (Urbaneja et al. 2012). Although chemical insecticides continue to be the main control option of this pest in many areas of the world, significant efforts have been made to develop IPM programs that use biological control (Castañé et al. 2011; Biondi et al. 2018; Desneux et al. 2022).

Successful biological control of this pest in the areas of the Mediterranean basin where it first invaded relies primarily on conservation biological control of the mirid bug predators *Macrolophus pygmaeus* (Rambur) and *Nesidiocoris tenuis* (Reuter) (Hemiptera: Miridae) (Desneux et al. 2022). Both are generalist predators that feed primarily on eggs, and the number of predated *T. absoluta* larvae is less than one per day from the second instar onwards (Urbaneja et al. 2009). Therefore, some studies have explored combining mirid predators with other natural enemies, such as hymenopteran larval or egg parasitoids, to extend the scope of biological control on this developmental stages of the pest (Urbaneja et al. 2012). To complement the poor action of these mirid predators on *T. absoluta* larvae, other studies have conducted surveys to identify native species of parasitoids targeting the larval stages (Zappalà et al. 2013; Gabarra et al. 2014; Ferracini et al. 2019).

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Numerous species of larval parasitoids of *T. absoluta* in the families Braconidae, Eulophidae, and Ichneumonidae have been recorded in Spain (Gabarra et al. 2014). *Necremnus tutae* Ribes & Bernardo (Hymenoptera: Eulophidae), previously cited as *Necremnus artynes*, is abundant in tomatoes across a wide geographical distribution (Gebiola et al. 2015). Thus, in many tomato-growing regions of Europe, conservation biological control using the widely distributed *N. tutae* could be a feasible strategy for controlling *T. absoluta* (Calvo et al. 2016; Crisol-Martinez & van der Blom 2019). Recently, Denis et al. (2022) made a groundbreaking observation by confirming the establishment of the neotropical parasitoid *Dolichogenidea gelechiidivoris* (Marsh) (Hymenoptera: Braconidae) in Europe for the first time, probably unintentionally introduced likely attributable to the dynamics of the tomato trade. This braconid is native to South America, where it is an important biological control agent of *T. absoluta* (Salas Gervassio et al. 2019). According to Denis et al. (2022), the presence of this larval parasitoid has been consistently documented in samples collected from commercial tomato crops in Catalonia (North-eastern Spain) spanning from 2016 to the present. Its spontaneous occurrence has also been detected in several tomato-growing regions in Algeria (Krache et al. 2021).

These two parasitoids have different biological attributes. *Necremnus tutae* is a gregarious idiobiont ectoparasitoid that prefers to parasitize 2nd to 3rd instar larvae of *T. absoluta* (Calvo et al. 2016; Bodino et al. 2019). *Dolichogenidea gelechiidivoris* is a solitary koinobiont endoparasitoid (Bajonero et al. 2008) that keeps the host alive until the end of parasitoid development and prefers to parasitize 1st and 2nd instars of *T. absoluta* (Aigbedion-Atalor et al. 2020). Both parasitoids can induce additional mortality by killing and feeding on the host (Ferracini et al. 2012; Balzan & Wäckers 2013; Chailleux et al. 2014; Calvo et al. 2016; Zhang et al. 2022a; Gonthier et al. 2023). Although many studies have examined the biology, host preference, and effectiveness of *D. gelechiidivoris* (Bajonero et al. 2008; Aigbedion-Atalor et al. 2020; Mama Sambo et al. 2022), no research has been conducted to elucidate the potential of plant-derived food sources in *D. gelechiidivoris* as a biological control agent of *T. absoluta.*

Plant-derived food sources (i.e., nectar, extrafloral nectar, plant guttation, and honeydew) play a crucial role in enhancing the presence of natural enemies in conservation biological control programs (Wäckers et al. 2008; Benelli et al. 2017; Urbaneja-Bernat et al. 2020, 2024; Fernández de Bobadilla et al. 2024). Specifically, these plant-derived food sources are the main sources of carbohydrates and protein for parasitoids in field conditions (Tena et al. 2016; Arnó et al. 2018; Urbaneja-Bernat et al. 2020, 2023). Different authors have studied the impact of plant-derived food sources in larval parasitoids of *T. absoluta*. For example the presence of *Macrosiphum euphorbiae* (Thomas) (Hemiptera: Aphididae) honeydew may benefit the biological control of the pest by *N. tutae* under laboratory and field conditions (de Campos et al. 2020). Also, previous studies on floral resources, such as *Lobularia maritima* (L.) Dev. (Brassicaceae), have shown that nectar sugar content positively influences the survival and reproduction of several natural enemies (Badenes-Pérez 2019) including some larval parasitoids of *T. absoluta* such as the eulophid *N. tutae* and the braconid *Bracon* sp. nr. *nigricans* Szépligeti (Tompkins et al. 2010; Balzan & Wäckers 2013; Aparicio et al. 2018; Arnó et al. 2018; Chen et al. 2020). In a field study conducted in 2019, several eulophids, including *N. tutae*, and braconids were observed on *L. maritima* flower strips near a tomato field. Among the braconids, 40% were identified as *D. gelechiidivoris* (Denis, Arnó, Riudavets unpublished). Besides, *L. maritima* is widely distributed in the Mediterranean basin. This, along with its long flowering period (Picó & Retana 2001), makes this floral resource ideal for promoting these parasitoids in tomatoes.

However, the effect of *L. maritima* on the performance (i.e., survival, parasitism, host feeding/killing, food/host foraging) of *N. tutae* and *D. gelechiidivoris* against *T. absoluta* remains poorly understood. Since it was demonstrated that floral resources could enhance the fitness (i.e., longevity, egg load) and performance of other parasitic wasps, we expected that feeding on *L. maritima* would enhance the fitness of *D. gelechiidivoris* and the performance of *N. tutae* and *D. gelechiidivoris*, thus enhancing the biological control action against *T. absoluta*. We used two main research questions to explore this hypothesis: (i) Does this floral resource affect the fitness of *D. gelechiidivoris*? (ii) Does *L. maritima* affect the performance of *N. tutae* and *D. gelechiidivoris*? We used a simple and complex microcosm arenas model of agricultural interest (herbivore – plant – natural enemy) to answer this last question.

2 Material and methods

2.1 Plant material and insects

All experiments and insect rearings were conducted at the Institut de Recerca i Tecnologies Agroalimentaries (IRTA) facilities (Cabrils, Barcelona, Spain) at a temperature of 25 ± 1 °C, relative humidity (RH) of 70 ± 10%, and a photoperiod of 16:8 h (L:D). Pesticide-free tomato plants (*cv*. Roma; Semillas Fitó) were grown from seeds in trays with multiplication substrate and kept in a greenhouse until the plants were used (30 cm high). *Tuta absoluta* larvae were reared on caged tomato plants (47.5 cm × 47.5 cm × 47.5 cm; BugDorm-2; MegaView Science, Taiwan). Adult females and males of the parasitoids *N. tutae* and *D. gelechiidivoris* were then released on caged tomato plants infested with *T. absoluta*. To obtain individuals, leaflets with parasitized *T. absoluta* larvae were kept in aerated cages until the parasitoids emerged. Herbivore and parasitic wasp colonies were initiated using individuals collected from commercial tomato fields infested with *T. absoluta* in North-eastern

Spain (Maresme County) and were refreshed annually. The *L. maritima* flowers used in the experiments were collected from plants grown in pots under greenhouse conditions.

2.2 Effect of *Lobularia maritima* on *D. gelechiidivoris* fitness

To study the effect of *L. maritima* on the longevity of *D. gelechiidivoris* females, four diets (treatments) were tested on newly emerged wasps (< 12 h): (i) water only, (ii) sugar only (1 M sucrose), (iii) sugar + protein (1 M sucrose + 1 M yeast extract) (1:1), and (iv) *L. maritima* flowers. Sucrose and sucrose + protein were used as control diets. The tested concentrations of sugar and protein were selected based on previous studies (Benelli et al. 2017; Urbaneja-Bernat et al. 2020, 2023). The experimental setup consisted of a plastic cup (350 cm^3, 50 mm diameter, 60 mm height) covered with a fine mesh that was fixed with a rubber band to allow ventilation. Several small drops (*ad libitum*) of sugar and sugar + protein were provided in each cup on a 1 cm^2 piece of Parafilm®. When required, floral nectar was supplied using an inflorescence of *L. maritima* (~50 open flowers) in an Eppendorf tube with water. Diets were renewed daily. Individual survival was checked daily until the parasitoids died. Twenty replicates were performed per each treatment.

To determine the effect of diets on egg load, newly emerged males and females (< 12 h) were placed inside a transparent, cylindrical plastic cup (946 ml; diameter, 114 mm; height, 127 mm; Paper Mart, CA, USA) and were provided one of the four diets (*ad libitum*) described above for 24 h to ensure mating. After 24 h (day 1), 15 females per diet were killed and maintained at −20°C. Another 30 females per diet were individually placed in a plastic cup similar to the ones used in the survival experiment, with the corresponding diet offered *ad libitum*. After 3 and 7 days, females (N = 15 diet/ day) were killed at −20°C. Therefore, we had newly emerged females (< 12 h), 1-, 3-, and 7-days old fed on the four different diets. The females were frozen at −20°C to measure the egg load by placing the wasp in a water drop under a stereomicroscope. The ovaries were squeezed out of the abdomen by placing light pressure on the thorax with pins. The ovaries were photographed, and the number of mature eggs was counted. The egg load of fifteen females for each diet and age was measured.

2.3 Effect of *L. maritima* in a simple arena

We evaluated the effect of *L. maritima* on *N. tutae* and *D. gelechiidivoris* parasitism with high *T. absoluta* density in a simple arena that the parasitoids did not need to search for host larvae. The experimental setup consisted of a plastic cup (same as in section 2.2; 350 cm^3) containing an isolated tomato leaflet and covered with a fine mesh fixed with a rubber band for ventilation. The cup had a small hole at the bottom to insert the tomato petiole. This plastic cup was placed inside a smaller one (230 cm^3) containing water to maintain the leaflet turgidity.

Each tomato leaflet (leaf area ~14 cm^2) was infested with ten *T. absoluta* larvae using a fine paintbrush. In accordance with the preferences reported in the literature, 2nd to 3rd-instar *T. absoluta* larvae were used for the experiments with *N. tutae* (Zhang et al. 2022b), and 1st–2nd-instar larvae were used for the bioassays with *D. gelechiidivoris* (Aigbedion-Atalor et al. 2020). Once the larvae had penetrated the leaf (after a maximum of ~5 h), a pair (male and female) of one- to ten-day-old *N. tutae* and a pair of one- to five-day-old *D. gelechiidivoris* that had fasted for the previous 24 h (provided only water) were released and kept in their respective cages for 48 h. In this experiment, we used parasitic wasps of different ages due to the considerable difference in adult longevity of both species, ~20 days for *N. tutae* and ~9 days for *D. gelechiidivoris* (Balzan & Wäckers 2013; Aigbedion-Atalor et al. 2020). Forty-eight hours after the parasitoids were released, the numbers of living and dead *T. absoluta* larvae were recorded. Moreover, in the cages with *N. tutae*, the number of ectoparasitized (paralyzed and with pupae, larvae, or eggs of the parasitoid on them) were scored separately. The experimental setups were kept under controlled conditions (same as above) until the parasitoids emerged. To evaluate the effect of *L. maritima* on parasitism, three treatments were compared: (i) larvae of *T. absoluta* + parasitic wasp, (ii) larvae of *T. absoluta* + parasitic wasp + *L. maritima*, and (iii) only larvae of *T. absoluta* (control). When required, floral nectar was supplied using an inflorescence of *L. maritima* (~50 open flowers) in an Eppendorf tube with water. We performed 15 replicates per each treatment.

2.4 Effect of *L. maritima* in a complex arena

A complex microcosm experiment was conducted in larger arenas using the BugDorm cages as described above (107×10^3 cm^3) to evaluate the impact of the *L. maritima* flower as a food source on the parasitism of both parasitoids species. Twenty tomato seedlings with four to six leaves each were introduced in each cage (leaf area ~252 cm^2). Ten larvae were carefully transferred to ten plants using a fine paintbrush (one larva/plant); ten plants received no *T. absoluta* larvae. Similar to the experiment in a simple arena (section 2.3), 2nd–3rd-instar *T. absoluta* larvae for *N. tutae* and 1st–2nd-instar *T. absoluta* larvae for *D. gelechiidivoris* were used.

A bunch of *L. maritima* (150 to 200 open flowers) was put in a 50 ml pot containing water, and the surface was sealed with cotton and kitchen plastic wrap to prevent wasp contact with the water; this pot was placed in the middle of the cage. These flowers were introduced to the appropriate cages, resulting in the same three treatments as in section 2.3. Once the larvae had penetrated the leaf, a pair of one- to five-day-old parasitoids that was given water access for 24 h were introduced to each cage without *L. maritima* (*T. absoluta* larvae + parasitic wasp). A pair of the same age that was given access to *L. maritima* flowers for the previous 24 h was released in each cage with a bunch of *L. maritima* flower (*T. absoluta* larvae + parasitic wasp + *L. maritima*).

Forty-eight hours after the parasitoids were released, the numbers of living and dead *T. absoluta* larvae were recorded. Moreover, in the cages with *N. tutae*, the number of ectoparasitized were scored separately. The egg load of surviving *N. tutae* females was also assessed. All plant material was then kept in aerated cages until the emergence of adult parasitoids, which were counted. For each of the three treatments, we performed 18 and 15 replicates for *N. tutae* and *D. gelechiidivoris*, respectively.

2.5 Statistical analyses

To analyze the effect of *L. maritima* on *D. gelechiidivoris* fitness, survival curves were analyzed using Kaplan–Meier survival analysis, followed by a log-rank test of equality. To test differences among diets, the number of mature eggs (egg load) at different days after emergence, we used generalized linear models (GLMs) assuming a Poisson distribution and a log link function. Also, the effect of *L. maritima* on both parasitic wasp species performance, was analyzed using GLMs assuming Poisson error distribution and a logit link function to analyze the percentage of *T. absoluta* larvae that were classified as alive, or dead, and the progeny of both parasitic wasps at high and low densities of *T. absoluta*. We then compared the fixed factor levels pairwise using the Bonferroni post hoc test ($P < 0.05$) upon a significant effect. Furthermore, differences in the number of ectoparasitized larvae (*N. tutae*) and the percentage of *D. gelechiidivoris* emerged were analyzed using Student's t tests. All analyses were conducted using SPSS 23.0.

3 Results

3.1 Effect of *Lobularia maritima* on *D. gelechiidivoris* fitness

Access to sugary foods increased the longevity of *D. gelechiidivoris* females ($\chi^2 = 51.4$, $P < 0.001$; Fig. 1a). *Dolichogenidea gelechiidivoris* longevity was higher among those fed on sugar only than those fed on *L. maritima* ($\chi^2 = 5.28$; $P = 0.021$). However, longevity on *L. maritima* was similar to that on sugar + protein ($\chi^2 = 2.57$; $P = 0.109$). Furthermore, there were not significant differences between longevity of wasps feeding on the two sucrose diets tested ($\chi^2 = 0.45$; $P = 0.832$).

Newly emerged females of *D. gelechiidivoris* (< 12 h) had an egg load of 60.8 ± 4.94 eggs per female. One day after their emergence, the egg load of *D. gelechiidivoris* females differed significantly depending on diet ($F_{3,\,60} = 88.48$, $P < 0.001$); those fed on *L. maritima* had the higher egg loads among all the treatments (Fig. 1b). Three days after wasp emergence, its egg load was similar in all diets tested ($F_{3,\,45} = 4.65$, $P = 0.098$). Females fed only on water died by the third day. Seven days after their emergence, *D. gelechiidivoris* females which fed on sugar or sugar + protein had significantly higher egg loads than those fed on *L. maritima* ($F_{3,\,45} = 120.24$, $P < 0.001$). There were no significant differences in the egg loads of females fed on either of the two sucrose diets.

3.2 Effect of *L. maritima* on *N. tutae* performance

The presence of *N. tutae* at high *T. absoluta* densities in a simple arena significantly affected the percentage of living ($F_{2,\,43} = 1196.5$, $P < 0.001$) and dead ($F_{2,\,43} = 965.1$, $P < 0.001$) *T. absoluta* larvae (Fig. 2: simple arena with high host density). Compared to the control, both treatments with *N. tutae* (with and without *L. maritima*) had lower percentages of living ($F_{2,\,28} = 2.14$, $P = 0.190$) and higher percentages of dead ($F_{2,\,28} = 2.58$, $P = 1$) *T. absoluta* larvae. Moreover, *L. maritima* availability did not impact the percentage of ectoparasitized larvae ($t = 0.404$, $df = 28$, $P = 0.69$), accounting for 40% and 45% in treatments with and without the floral resource, respectively.

In complex microcosm studies, the presence of the parasitoid at low *T. absoluta* densities significantly reduced the percentage of living ($F_{2,\,54} = 24.12$, $P < 0.001$) *T. absoluta* larvae, and increased the percentage of dead larvae compared to the control ($F_{2,\,54} = 35.75$, $P < 0.001$) (Fig. 2:

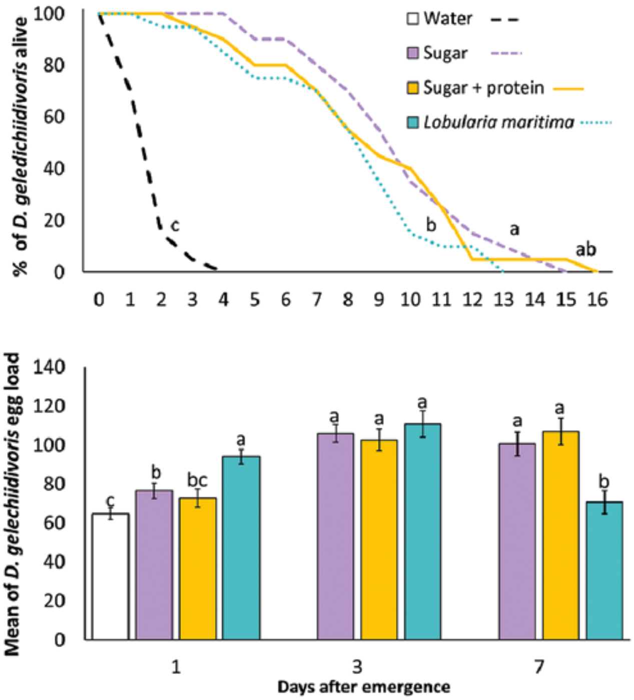

Fig. 1. Survival curves for *Dolichogenidea gelechiidivoris* (top graph) fed on four different diets: water and sugar only (1 M); sugar + protein, and *Lobularia maritima* (different letters indicate significant differences among the treatments according to the log-rank test of equality) and mean number (± SE) of mature eggs in *D. gelechiidivoris* (bottom graph) fed on the four different diets for one, three, and seven days after adult emergence (different letters indicate significant differences among treatments according to the Bonferroni pairwise tests).

Complex microcosm arena with low host density). However, *L. maritima* did not affect the percentage of living ($F_{2, 34} = 2.11$, $P = 1$) and dead ($F_{2, 34} = 2.05$, $P = 1$) *T. absoluta* larvae. Furthermore, access to *L. maritima* did not affect the percentage of ectoparasitized larvae ($t = 0.68$, $df = 34$, $P = 0.947$), being ~11% in both treatments. Considering the *N. tutae* parasitism results obtained in the simple arena and complex microcosm studies, the fitness evaluation in terms of the number of mature eggs (egg load) per female recovered alive were recorded. The results showed that females that fed on *L. maritima* exhibited a remarkable 1.5-fold increase in egg load compared to females that were not provided with *L. maritima* (6.1 ± 0.7 vs. 3.9 ± 1.4). However, it is noteworthy that statistical analysis did not reveal any significant differences ($t = 4.08$, $df = 22$, $P = 0.126$) between the two groups. Survival of *N. tutae* females in the microcosms with *L. maritima* (~78%) was double that in cages without flowers (~39%; $t = 4.39$, $df = 34$, $P = 0.017$).

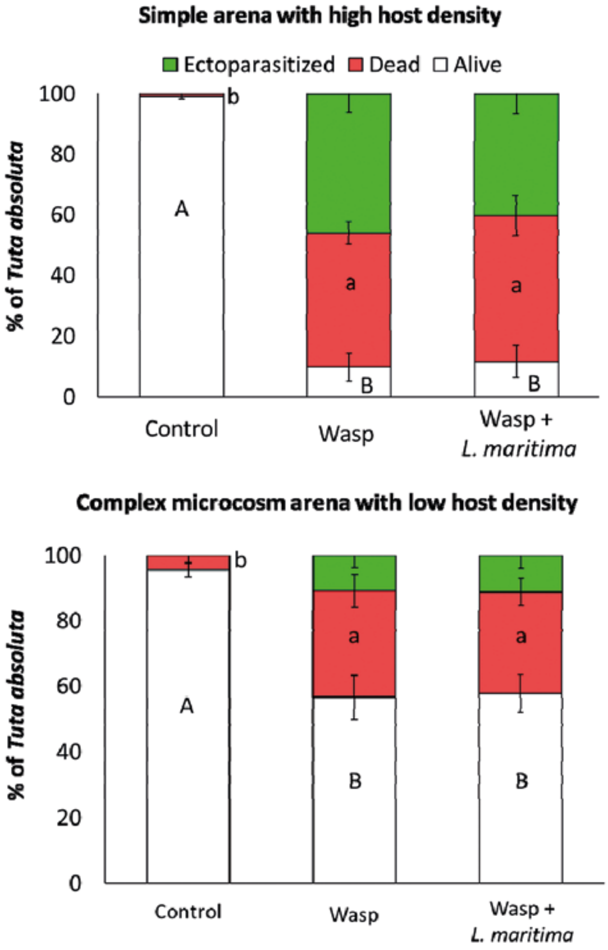

Fig. 2. Percentage of living, dead, and ectoparasitized (by *Necremnus tutae*) *Tuta absoluta* larvae in simple and complex microcosm arenas. Different capital and lowercase letters indicate significant differences in living and dead larvae, respectively (Bonferroni $P < 0.05$). No significant differences in the number of ectoparasitized larvae were found (*t*-test $P < 0.05$).

3.3 Effect of *L. maritima* on *D. gelechiidivoris* performance

The presence of *D. gelechiidivoris* at high *T. absoluta* densities in a simple arena significantly influenced the percentage of living ($F_{2, 43} = 105.2$, $P < 0.001$) and dead ($F_{2, 43} = 140$, $P < 0.001$) *T. absoluta* larvae (Fig. 3: Simple arena with high host density). The percentage of living *T. absoluta* larvae was lower in both treatments with the parasitoid (with and without *L. maritima*) than in the control, and the number of dead larvae was higher. When the treatments with the parasitoid were compared, *L. maritima* did not significantly impact the number of living ($F_{2, 28} = 17.98$, $P = 0.095$) or dead ($F_{2, 28} = 0.11$, $P = 1$) larvae. *Lobularia maritima* availability also did not affect the percentage of larvae from which an adult wasp emerged (% parasitism) ($t = 14.53$, $df = 24$, $P = 0.358$); an adult *D. gelechiidivoris* emerged from 51% vs. 40% of larvae with and without the floral resource, respectively.

In complex microcosm studies, the presence of the parasitoid at low *T. absoluta* densities significantly reduced the

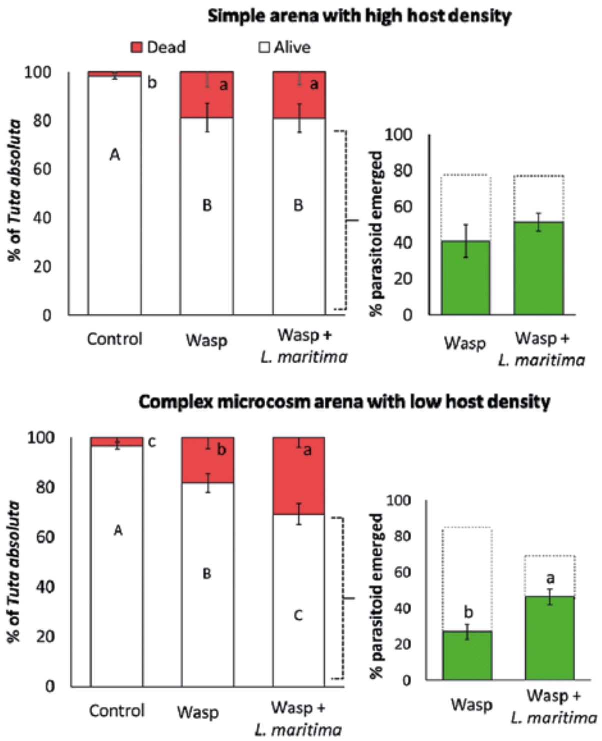

Fig. 3. Percentage of living and dead *Tuta absoluta* larvae (left graphs) and percentage of larvae from which an adult of *D. gelechiidivoris* emerged (right graphs) in simple and complex microcosm arenas. Different capital and lowercase letters indicate significant differences in living and dead larvae (Bonferroni $P < 0.05$). Different letters indicate significant differences in the percentage of *D. gelechiidivoris* that emerged (*t*-test $P < 0.05$).

percentage of living *T. absoluta* larvae ($F_{2,\,39} = 246.8$, $P < 0.001$). It increased the percentage of dead larvae ($F_{2,\,39} = 54.01$, $P < 0.001$) compared to the control (Fig. 3: Complex microcosm arena with low host density). When we compared the treatments with and without *L. maritima*, the number of living ($F_{2,\,39} = 33.14$, $P < 0.001$) and dead ($F_{2,\,39} = 295.73$, $P = 0.022$) *T. absoluta* larvae differed significantly. Survival of *D. gelechiidivoris* females in the microcosms with *L. maritima* was higher (~58%) than that in cages without flowers (~23%), but this difference was not significant ($t = 1.84$, $df = 25$, $P = 0.075$). *Lobularia maritima* availability also positively influence the percentage of parasitism ($t = 3.58$, $df = 25$, $P = 0.001$); an adult *D. gelechiidivoris* emerged in 47% vs. 27% of larvae in the treatments with and without the floral resource, respectively. Then, due to the strong observed effect of *L. maritima* on *D. gelechiidivoris* parasitism, in this case the number of mature eggs were not recorded.

4 Discussion

Many studies have demonstrated the positive effect of different nutritive plant-derived food sources on the biological parameters of parasitoids (Heil 2015; Tena et al. 2016; Urbaneja-Bernat et al. 2020; Wäckers et al. 2005). More specifically, the carbohydrates in flower nectar are vital for parasitoid longevity (Irvin et al. 2007; van Rijn & Wäckers 2016). However, not all flowering species provide food resources of equal quality for a particular parasitoid (Arnó et al. 2018). These last authors and Balzan and Wackers (2013) have demonstrated the positive impact of *L. maritima* on the fitness of *N. tutae*, one of the species included in our study. Our results show that *L. maritima* also improves *D. gelechiidivoris* fitness. These findings align with earlier studies that found that *L. maritima* benefits other braconid parasitoid species, such as *Aphidius ervi* (Aparicio et al. 2018; Chen et al. 2020). As we expected, both parasitic wasps, regardless of whether or not they needed to forage for the host (simple vs. complex microcosm arenas), produced high pest mortality, not only by parasitizing but also by feeding and killing the host. As mentioned, several studies have recognized *N. tutae* as a parasitoid that predominantly feeds on the host. More recently, Gonthier et al. (2023) have reported that *D. gelechiidivoris* kills and feeds on the host. Synovigenic parasitoids, such as *N. tutae* and *D. gelechiidivoris*, require additional protein for egg maturation, which they obtain by feeding on the hemolymph of the host (Casas et al. 2005; Fischer et al. 2007).

Availability of *L. maritima* positively influenced the performance of both parasitic wasps in the complex microcosm arenas when they needed to forage for *T. absoluta* larvae but had a negligible effect in simple arenas with high host densities. Although the positive effect of *L. maritima* on *N. tutae* survival has been previously demonstrated (Arnó et al. 2018; Balzan & Wackers 2013) in the absence of prey, our results indicate that, in conditions of high host density, the presence of this floral resource does not increase the number of dead or parasitized *T. absoluta* larvae. Furthermore, *L. maritima* did not reduce *N. tutae* ability to search for the host in complex microcosm arenas with low host densities, at least in this short-term experiment (48 h), because the same amounts of parasitized and dead *T. absoluta* larvae were recorded in treatments with and without *L. maritima*. However, in the presence of the flower resource, the survival of females significantly increased, and egg load tended to be higher, suggesting a positive effect on pest control in the medium and longer term. In contrast, *L. maritima* does improve the search capacity of *D. gelechiidivoris* in the complex microcosm arenas with low host density. The presence of the floral resource more than doubled the survival of foraging females and significantly increased the progeny and the number of dead and parasitized larvae. These findings are consistent with other studies demonstrating that the performance of hymenopterans is determined by the type of sugar and protein in their diets (Wäckers et al. 2005; Tena et al. 2016; Urbaneja-Bernat et al. 2024).

In conclusion, our results demonstrate that the nectar of *L. maritima* is a nutrient-rich food source for *N. tutae* and *D. gelechiidivoris*. This study provides the first evidence that this flowering species enhances the performance of *D. gelechiidivoris* and significantly reduces the percentage of live *T. absoluta* larvae in tomatoes. Furthermore, these results highlight the importance of sugary foods in foraging behavior of the wasps, essential to successfully controlling pests from the early stages of attack (Heimpel 2019). Based on other studies on floral resources with natural enemies, access to these nutritive sources significantly improves the biological parameters of parasitoids (Lewis et al. 1998; Lee & Heimpel 2008). However, there are still some unanswered questions about the effect of *L. maritima* on these parasitic wasps, such as the nutritional profile of carbohydrates and proteins in the plant nectar and the odors/volatiles of *L. maritima* that may attract these two parasitic wasps and *T. absoluta*. Other studies have shown that the volatiles of *L. maritima* have positive effects on the adults of other parasitic wasps, such as *Cotesia vestalis* (Chen et al. 2020). Future studies should also assess the possible long-term effects of *L. maritima* on these parasitic wasps during the tomato growing season. We conclude that access to *L. maritima* may positively influence *N. tutae* and *D. gelechiidivoris* populations in tomatoes. Further field studies are needed to determine the overall effect of this floral resource on improving the biological control of *T. absoluta* in tomato crops.

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