



Effect of alternative nectar sources and herbivore-induced plant volatiles on the fitness and attraction of *Aphidoletes aphidimyza*

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Received: 22 July 2025 / Accepted: 18 September 2025 / Published online: 1 December 2025
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Abstract

Enhancing natural enemy populations in agricultural systems by combining habitat manipulation and herbivore-induced plant volatiles (HIPVs) offers a promising approach to conservation biological control. The aphidophagous midge *Aphidoletes aphidimyza* is widely used in biological control programs in many crops, and the development of novel attract and reward (A&R) strategy may promote the establishment and survival of *A. aphidimyza* in crops. Here, we focus on (i) the attractiveness (under laboratory conditions) to *A. aphidimyza* of the HIPVs phenylacetaldehyde (Pal) and methyl salicylate (MeSA) and plants in the families Brassicaceae, Euphorbiaceae, Asteraceae and Fabaceae, all evaluated separately, and (ii) the effect of consuming nectar from *Eruca vesicaria*, *Euphorbia segetalis*, *Moricandia arvensis*, *Calendula officinalis*, *Vicia faba*, *V. sativa*, *Medicago sativa*, and *Centaurea cyanus* on *A. aphidimyza* survival, as well as the impact of the first five species on egg load. Neither of the tested HIPVs (Pal and MeSA) induced a positive chemotactic response in double-choice bioassays, nor did any of the tested plants. Survival curves varied according to the food provided; *A. aphidimyza* females fed *V. faba*, *V. sativa* (Fabaceae), or *E. vesicaria* (Brassicaceae) had the highest survival rates, significantly higher than those of *A. aphidimyza* fed only water. Plant food sources also impacted egg load, which was significantly higher in females fed *C. officinalis* than in those fed *V. faba*; egg numbers in females fed *E. vesicaria* did not differ significantly from either. Together, these findings represent a first step toward determining the potential of insectary plants for improving *A. aphidimyza* performance.

Keywords *Myzus persicae* · *Dysaphis plantaginea* · *Vicia* spp. · Conservation biological control · Phenylacetaldehyde · Methyl salicylate

Introduction

The gall midge *Aphidoletes aphidimyza* (Rondani) (Diptera: Cecidomyiidae) is one of the most important aphid predators (Boulanger et al. 2019). This species is present across the Holarctic region and has also been reported in Chile, Brazil and New Zealand (Havelka and Zemek 1988; Aguilera

and Pacheco 1995; Yamane et al. 2012; Fidelis et al. 2018; Amokrane et al. 2024). Adults emerge from pupae in the soil and then fly to search for aphid colonies, where they lay eggs. After hatching, the larvae prey voraciously on aphids (Boulanger et al. 2019).

The gall midge is a polyphagous predator that preys on 85 aphid species, including many species with economic relevance (Boulanger et al. 2019). Therefore, *A. aphidimyza* is used in inundative and inoculative biological control programs against aphids in various crops, both in open air and in greenhouses (Boulanger et al. 2019; Riudavets et al. 2020). *A. aphidimyza* has been reported to successfully reduce aphid populations in various regions worldwide and in a wide range of crops, including vegetables, ornamental crops, citrus fruits, and apples (Stewart and Walde 1997; Solarska 2004; Abe et al. 2011; Gómez-Marco et al. 2016; Jandricic et al. 2016; Boulanger et al. 2019).

Communicated by Ramzi Mansour.

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Aphids such as *Myzus persicae* (Sulzer) (Hemiptera: Aphididae), *Dysaphis plantaginea* (Passerini) (Hemiptera: Aphididae), and *Hyalopterus pruni* (Geoffroy) (Hemiptera: Aphididae) are important pests in fruit orchards (Guerrieri and Digilio 2008; Barbagallo et al. 2017). Even though several natural enemies have been reported to attack these aphids, biological control rarely prevents outbreaks, probably because the presence of both predators and parasitoids is a consequence of high aphid populations (Dedryver et al. 2010; Simon et al. 2010).

Colonies and honeydew from aphids have been shown to attract natural enemies (El Titi 1974; Choi et al. 2004; Watanabe et al. 2016; Jandricic et al. 2016), but in the early stages of pest crop colonization, when aphid colonies and honeydew are scarce, planting insectary plants and/or releasing synthetic herbivore-induced plant volatiles (HIPVs) could offer alternative methods for attracting natural enemies into orchards (Higashida et al. 2016, 2022; Rodríguez-Gasol et al. 2019; Aparicio et al. 2021). Both insectary plants and HIPVs are key elements of the attract and reward (A&R) strategy, which aims to enhance biological control by first recruiting natural enemies from surroundings habitats and then promoting their populations by providing the necessary resources (i.e., food and shelter) for their successful development (Simpson et al. 2011).

Thus, many insectary plants are used in flower strips to provide food for natural enemies (Laubertie et al. 2012; Zhou et al. 2014; Arnó et al. 2018; Denis et al. 2021). Strips of insectary plants from the families Brassicaceae and Asteraceae increase the abundance of natural enemies of *D. plantaginea* (Rodríguez-Gasol et al. 2019) and *M. persicae* (Aparicio et al. 2021) when placed near apple and peach orchards, respectively. When choosing potential insectary plants to attract and reward *A. aphidimyza*, nectar accessibility is an important criterion (Branquart and Hemptinme 2000; Wäckers et al. 2007; van Rijn and Wäckers 2016), because the long legs of *A. aphidimyza* adults make it difficult for them to obtain nectar from some flowers (Aparicio et al. 2018). Another important criterion is that the insectary plants should flower in the early spring (Denis et al. 2021) to provide food resources (nectar), as aphid populations and honeydew are scarce at the beginning of the season. However, in Neotropical regions, food resources are generally available year-round (Ramalho et al. 1990), and therefore, this criterion is not strictly necessary.

HIPVs deserve attention in biological control approaches due to their key role in the tritrophic interactions among plants, pests, and natural enemies (Turlings and Erb 2018). HIPVs are low molecular weight compounds from different functional groups; they include terpenoids, phenylpropanoids/benzenoids, and fatty acid and amino acid derivatives. Species-specific blends are released in large quantities when plants are affected by an herbivore that triggers indirect plant

defenses. HIPVs elicit different responses within tritrophic interactions, and this chemical signaling is not limited to interspecific effects, as HIPVs have been reported to act as chemical messengers for neighboring undamaged plants, triggering their defenses (Paudel Timilsena et al. 2020). HIPVs also deter feeding and oviposition in pest insects (Kessler and Baldwin 2001), in addition to attracting natural enemies (Yasa et al. 2024; Michereff et al. 2024). Natural enemies exploit these plant-related chemical cues as synomones that allow them to locate their hosts, benefiting both the natural enemy and the attacked plant. Here, we focus on phenylacetaldehyde (Pal) and methyl salicylate (MeSA) as potential attractants for *A. aphidimyza* females, as these HIPVs have been shown to attract other natural enemies in a number of insect orders (Orre et al. 2010; Simpson et al. 2011; Watanabe et al. 2016; Pålsson et al. 2022; Twidle et al. 2022). In addition, a blend of Pal, MeSA and acetic acid has been shown to strongly attract green lacewings (Neuroptera: Chrysopidae) under field conditions (Tóth et al. 2009).

Pal is a volatile compound released by flowers; it is also present in the honeydew of *Aphis gossypii* Glover (Hemiptera: Aphididae) (Knudsen et al. 1993; Watanabe et al. 2016). MeSA is a plant volatile that is released in response to insect damage by a wide range of plants, including aphid-infested apple trees (Kaplan 2012; Badra et al. 2021; Russavage et al. 2024) and some flowers (Effmert et al. 2008; Das et al. 2013). Both Pal and MeSA are reported to elicit strong electroantennographic responses in *A. aphidimyza* (Molnár et al. 2018). However, the capacity of these HIPVs to attract *A. aphidimyza* has been poorly studied. In fact, only Watanabe et al. (2016) have reported that Pal attracts this predator, and no previous study has examined the potential of MeSA to attract *A. aphidimyza*.

To the best of our knowledge, the use of insectary plants to attract and reward *A. aphidimyza* has only been evaluated for *Lobularia maritima* (L) (Brassicaceae) (Aparicio et al. 2018), and little is known about the capacity of HIPVs to attract this predator (Watanabe et al. 2016). Therefore, the present study aims (i) to evaluate several Mediterranean plant species as potential nectar sources and attractants for *A. aphidimyza* and (ii) to evaluate Pal and MeSA as potential attractants for *A. aphidimyza*.

Materials and methods

Natural enemy

Commercial *A. aphidimyza* (Agrobio®, Almería, Spain) were used in all assays. Adults were obtained by keeping pupae under laboratory conditions (22 ± 1 °C; $80 \pm 3\%$ RH; photoperiod 16:8 h light/dark (L:D)) in aerated 1.8 L containers. Each container held a 7 mL glass vial filled with

water, cotton balls (1 cm diameter) were used as stoppers, and the vials were positioned upside down to moisten the cotton. *A. aphidimyza* females (< 24 h old) that emerged with males in the same containers and were assumed to be mated, and had not oviposited previously, were used in all the assays.

Volatiles (HIPVs)

The HIPVs were chosen based on their known attractiveness to *A. aphidimyza*. Pal is released from the honeydew of *A. gossypii* and has been shown to attract *A. aphidimyza* (Watanabe et al. 2016), while MeSA is released by apple trees infested by *D. plantaginea* (Badra et al. 2021), a prey of *A. aphidimyza*. Additionally, electroantennogram studies have shown that *A. aphidimyza* elicit strong responses to both Pal and MeSA (Molnár et al. 2018).

The HIPVs Pal (95%) and MeSA ($\geq 99\%$) were purchased from Sigma-Aldrich (St. Louis, MO, USA). Each compound was diluted in hexane ($\geq 95\%$, Sigma-Aldrich) (James 2006; Zhao et al. 2020) until the desired amount of the compound was present for each test. For each compound, four quantities from 0.1 μg to 100 μg were evaluated. The lowest quantity tested corresponded to the amount shown to be attractive to *A. aphidimyza* and used by Watanabe et al. (2016), but higher amounts were subsequently evaluated since no behavioral response was observed at this quantity. For the assays, 200 μL of the solution of each compound were loaded onto filter paper (2 $\times$ 2 cm, Branchia, BLPG-125-100, Barcelona, Spain) and placed inside a glass container (30 mL).

Nectar resources

Species of insectary plants were selected based on several factors: flowering in early spring (*Eruca vesicaria* L. (Brassicaceae), *Moricandia arvensis* DC (Brassicaceae), *Euphorbia segetalis* L. (Euphorbiaceae), and *Vicia faba* L. (Fabaceae)), the presence of extrafloral nectaries (*Centaurea cyanus* L. (Asteraceae), *E. segetalis*, *V. faba*, *Vicia sativa* L. (Fabaceae), and *Medicago sativa* L. (Fabaceae)), and composite flowers (*Calendula officinalis* L. (Asteraceae), and *C. cyanus*). These species are naturally present in the Mediterranean fruit tree-growing area in northeastern Spain (Associació Flora Catalana 2025) and have been reported to attract natural enemies (Arnó et al. 2012; Géneau et al. 2012, 2013; Alins et al. 2019; Rodríguez-Gasol et al. 2019; Denis et al. 2021). All insectary plants were grown outdoors in a field at IRTA, Cabrils (Catalonia, Spain), directly in soil with irrigation, without fertilization, kept free of aphids and other pests.

Attraction assays

The attraction response of *A. aphidimyza* was assessed using a double-choice Y-tube olfactometer (arm lengths = 17 cm; arm diameter = 3.5; angle between secondary arms = 75°; positioned horizontally) following the set-up described by Aparicio et al. (2018). Each secondary arm supplied airflow from one of the two odor sources that were placed inside the two glass containers (4 L) connected to them. Airflow was created using an ABAC-FC2-24CM compressor; the air passed through a double activated carbon filter (ABAC-ACF60 1.000 Lmh, ACFC 60 filter, maximum 16 bar, 35 °C; kit number 2258 2900 02; European Union) and a humidifier before entering into the glass containers (Aparicio et al. 2018). The airflow was set to $0.21 \pm 0.01 \text{ m} \times \text{s}^{-1}$ at the base of the main arm and was measured using a hot wire anemometer (Testo 454, Barcelona, Spain). Air temperature and relative humidity (RH) were monitored at the base of the main arm using a data logger (Testo 175T1, Lenzkirch, Germany) ($22.5 \pm 0.6 \text{ }^{\circ}\text{C}$; $64.5 \pm 7.4\% \text{ RH}$).

The olfactometer was placed in a controlled-temperature chamber set to 22 °C, and the entire system was homogeneously illuminated by a white light source (Sylvania circline FC22W/865, China), which was placed 20 cm above the Y-tube (Aparicio et al. 2018).

The following treatments were evaluated: Four different amounts (0.1, 1, 10, and 100 μg) of the HIPVs Pal and MeSA diluted in hexane ($\geq 95\%$, Sigma-Aldrich) were tested singly. A total of 200 μL from each dilution was placed on a 2 $\times$ 2 cm piece of laboratory filter paper (Branchia, BLPG-125-100, Barcelona, Spain) and placed inside a small glass vessel (30 mL). The glass vessel (30 mL) was kept closed until placed inside the 4-L glass containers and was replaced every 20 min throughout the assay for each amount. This interval was determined after preliminary assessments of the release rate.

While five insectary plants species were also tested singly (one *E. vesicaria* shoot with four to five flowers in anthesis, one *M. arvensis* shoot with four to five flowers in anthesis, one *E. segetalis* shoot with five to seven inflorescences in anthesis, one *C. officinalis* shoot with three capitula in anthesis, and one 5 cm *V. faba* stem with four to five extrafloral nectaries). All cut stems were immediately immersed in water after cutting and then placed inside a 4 L glass container 1 h before starting the assay. Fresh nectar resources from different, previously uncut plants were used for every assay. The response to each HIPV and plant species was compared to the response to clean air as a control.

The females (< 24 h old, emerged with males, and not oviposited previously) were used just after the end of scotophase in the morning and were released individually at the base of the main arm and left for 10 min (Aparicio et al. 2018). A choice was noted when a female flew or walked

more than 5 cm into one of the secondary arms (Aparicio et al. 2018). Each female was used only once. After every two insects, the arm position was switched to avoid any directional bias. For each HIPV 51–57 females and for each plant species 53–58 females, were tested. Females that did not make a choice within 10 min were excluded from the analysis.

Fitness trials

Survival

The survival of *A. aphidimyza* females was assessed in two independent assays conducted in a controlled climatic chamber (22 ± 1 °C; $80 \pm 3\%$ RH; 16:8 h L:D). In the first assay, the same nectar resources evaluated in the attraction assays were used: one *C. officinalis* capitulum, one *E. segetalis* inflorescence, two *E. vesicaria* flowers, two *M. arvensis* flowers, and one *V. faba* extrafloral nectary. In the second assay, the most promising nectar resource identified in the first assay (*V. faba*) and three additional plants with extrafloral nectaries were evaluated (one *V. sativa* shoot with two extrafloral nectaries, one *M. sativa* shoot with two extrafloral nectaries, and one *C. cyanus* capitulum with an extrafloral nectaries).

Both assays were conducted using a completely randomized design, with 16 and 15 repetitions of each assay, respectively. For each experimental unit, a single *A. aphidimyza* female was placed in an aerated glass container (750 mL) that held either a plant nectar resource, a 10% sugar solution (glucose, fructose, and sucrose at 1:1:1), or water. Each food source was supplied in a 7 mL glass vial with 1 cm of cotton serving as a stopper; the vials were positioned upside down to ensure the cotton remained moist. For the assays using plants, the plants were placed in vials filled with water to prevent wilt and were replaced every 3 days. The survival of the *A. aphidimyza* was monitored daily until all the females died.

Egg load

Egg load was evaluated under the same laboratory conditions as survival and using the same treatments and controls as the first survival experiment (*C. officinalis*, *E. segetalis*, *E. vesicaria*, *M. arvensis*, *V. faba*, sugar solution, and water). The trial was organized using a completely randomized design. *A. aphidimyza* emerged in cages with access to water, and each < 24 h old female was placed in an aerated glass container (750 mL) with water for another 24 h (Sell and Kuo-Sell 1987). Next, 40 of the females were provided with a plant nectar source, the sugar solution, or water for an additional 48 h. Afterward, the number of surviving females was recorded, and only the females found alive

were frozen. Egg load was determined by dissection under a stereomicroscope.

Statistical analysis

Differences in the attraction response of the *A. aphidimyza* females in olfactometric trials were evaluated using a two-sided binomial test conducted with SAS 9.4 (Belda and Riu-davets 2012; Aparicio et al. 2018). Survival data were analyzed using Kaplan–Meier survival curves, and the analyzed was performed using SAS 9.4. A log-rank test (adjusted using the Benjamini–Hochberg method, $\alpha = 0.05$) was used for pairwise comparisons of the survival curves and the pairwise survdiff function from the survminer package with the Bonferroni adjustment for multiple comparisons. Whereas egg load data were analyzed with a GLM using a quasi-Poisson distribution, with Tukey-adjusted pairwise comparisons. Treatments in which less than 25% the females survived were not included in the final analyses. These last tests were conducted in R version 4.4.0 (R Core Team 2021).

Results

Attraction assays

None of the tested amounts of HIPVs attracted *A. aphidimyza* females more than clean air, in fact, the females demonstrated significant preference for clean air compared with the lowest amount of Pal ($Z = 2.14$; $p = 0.0470$) (Figs. 1 and 2). Similarly, no preferences for any insectary plants were observed (Fig. 3). The females showed a significant preference for clean air over *M. arvensis* ($Z = 2.24$; $p = 0.0357$) (Fig. 3).

Fitness trials

Survival

In the first assay, different food resources led to significant differences in survival curves (log-rank chi-square = 43.97; $df = 6$; $p < 0.0001$) (Fig. 4, Table 1). Females fed on the sugar solution or on the EFN of *V. faba* had the highest survival probabilities, with no differences between these resources. Females fed on *E. vesicaria* were significantly more likely to survive than those fed on water, although they lived significantly shorter than sugar-fed females (Fig. 4, Table 1). *A. aphidimyza* females with access to *M. arvensis*, *E. segetalis*, and *C. officinalis* had similar survival curves that females with only access to water (Fig. 4, Table 1).

In the second assay, significant differences in survival probabilities were detected among feeding resources (log-rank chi-square = 45.41; $df = 5$; $p < 0.0001$) (Fig. 5, Table 2).

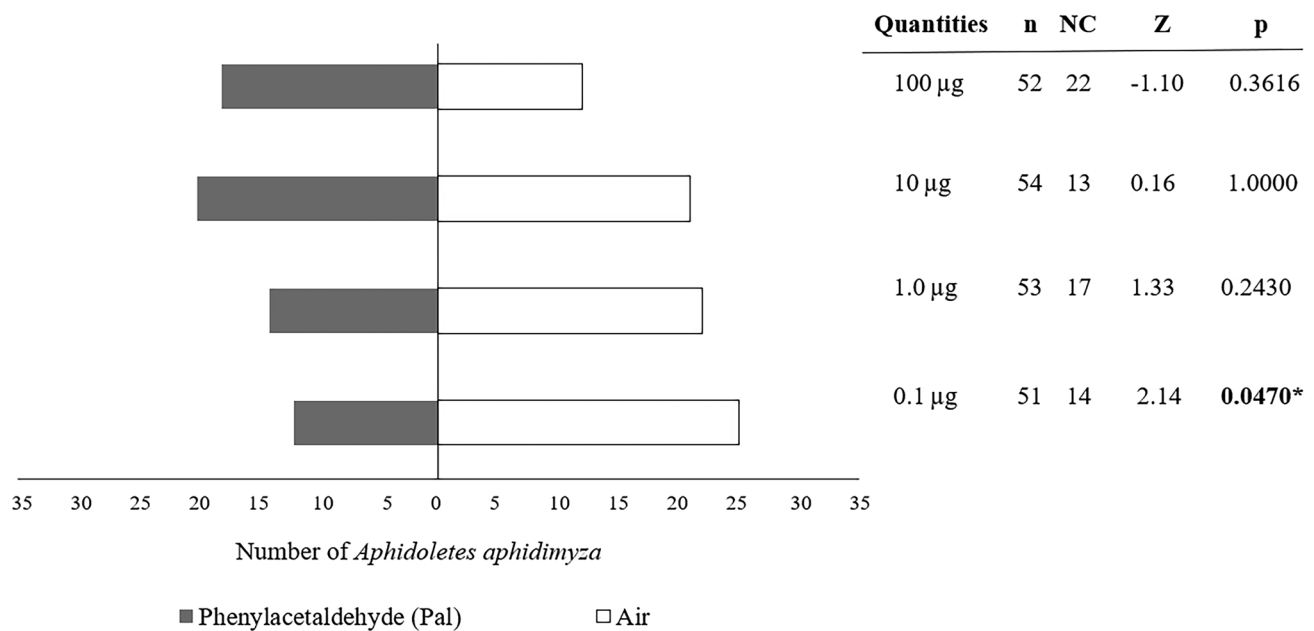


Fig. 1 Number of *Aphidoletes aphidimyza* females attracted to different quantities (0.1, 1, 10, or 100 µg) of Pal versus clean air in a Y-tube olfactometer; *n* = number of females evaluated; NC = number of females who did not choose any olfactometer arm and were not

included in the analysis; *Z* and *p* values refer to a two-sided binomial test. Bold font with an asterisk indicates a significant preference for a specific arm

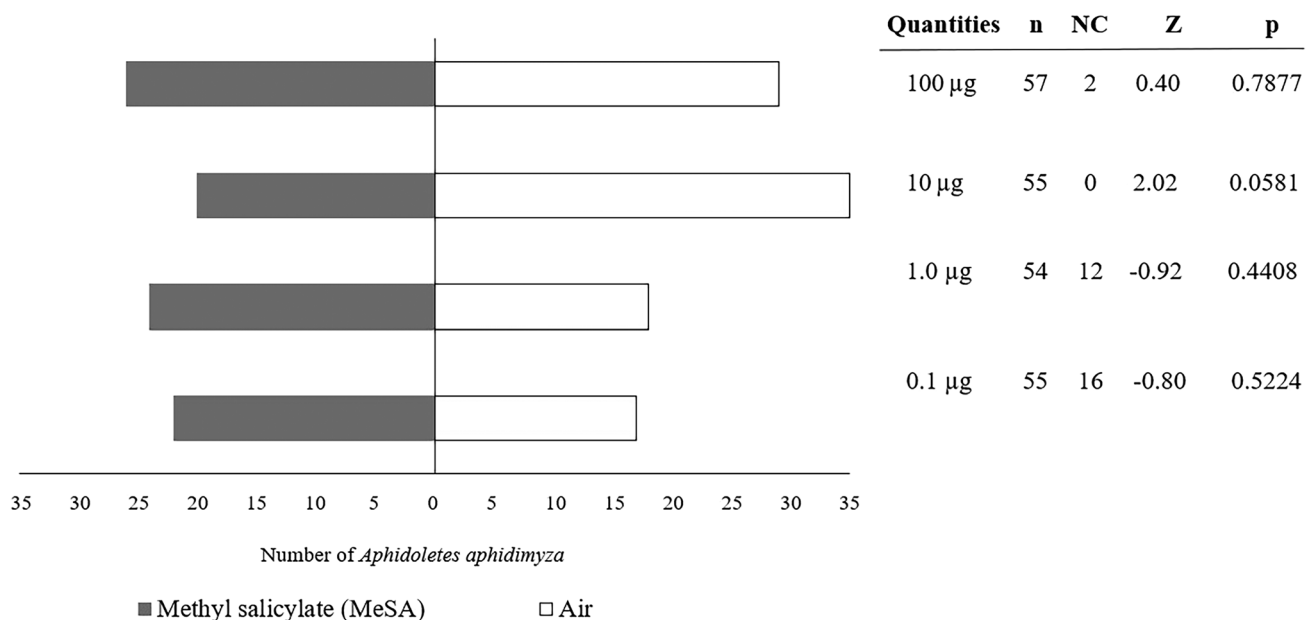


Fig. 2 Number of *Aphidoletes aphidimyza* females attracted to different quantities (0.1, 1, 10, or 100 µg) of MeSA versus clean air in a Y-tube olfactometer; *n* = number of females evaluated; NC = number

of females who did not choose any olfactometer arm and were not included in the analysis; *Z* and *p* values refer to a two-sided binomial test

The highest survival probabilities were observed for the sugar solution, *V. faba*, and *V. sativa*. These resources led to significantly higher survival curve than *M. sativa*, *C. cyanus*, and water (Fig. 5, Table 2).

Egg load

Females fed *C. officinalis* had significantly higher egg loads than those fed *V. faba* ($p = 0.0295$) (Fig. 6), while

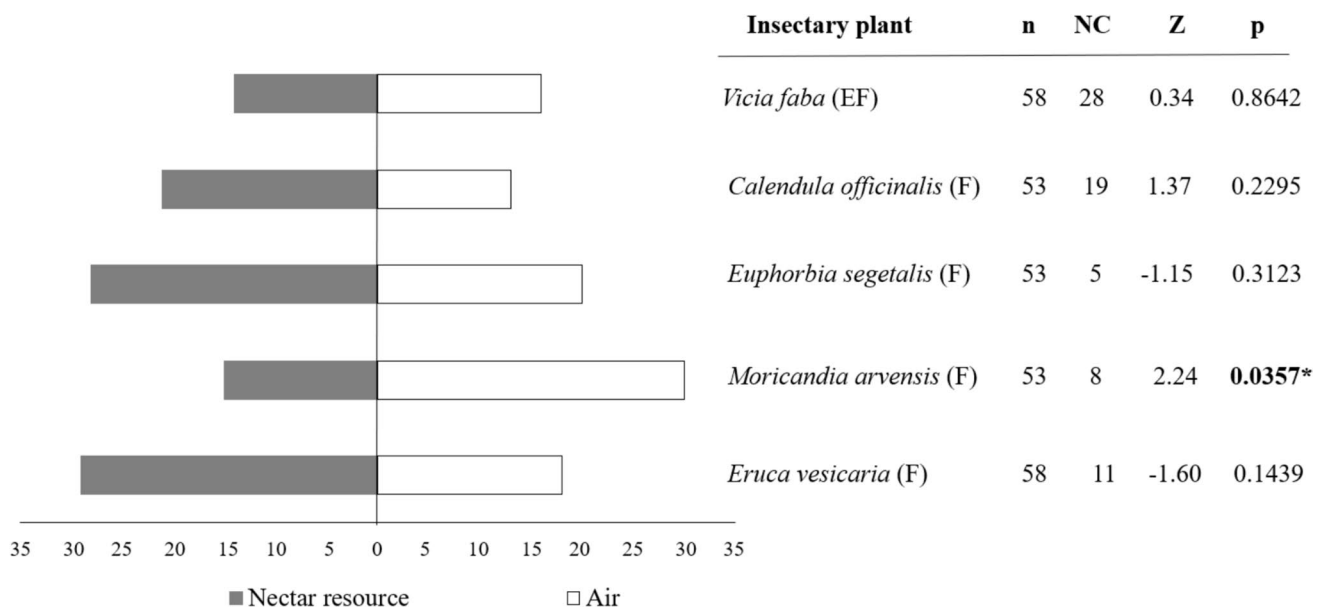


Fig. 3 Number of *Aphidoletes aphidimyza* females attracted to different plant species (EF=with extrafloral nectar; F=with floral nectar) vs. clean air in a Y-tube olfactometer; n =number of females evalu-

ated; NC=number of females that did not choose any olfactometer arm; Z and p values refer to a two-sided binomial test. Bold font with an asterisk indicates a significant preference for a specific arm

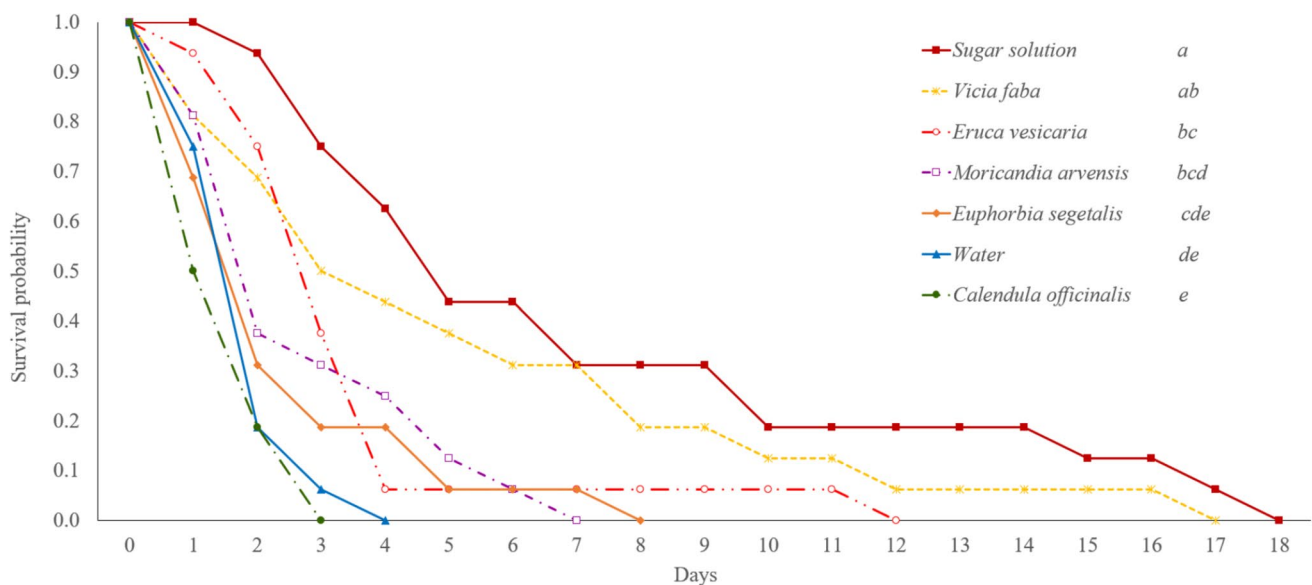


Fig. 4 Kaplan-Maier survival curves for *Aphidoletes aphidimyza* females (first assay) fed different floral and extrafloral nectars (*Calendula officinalis*, *Euphorbia segetalis*, *Eruca vesicaria*, *Moricandia arvensis*, or *Vicia faba*), a 10% sugar solution (glucose, fructose, and sucrose at 1:1:1), or water under laboratory conditions (22 ± 1 °C;

$80 \pm 3\%$ RH; 16:8 h L:D). Different letters indicate significant differences among food sources based on a pairwise comparison of survival curves (log-rank test adjusted using the Benjamini-Hochberg method, $\alpha=0.05$)

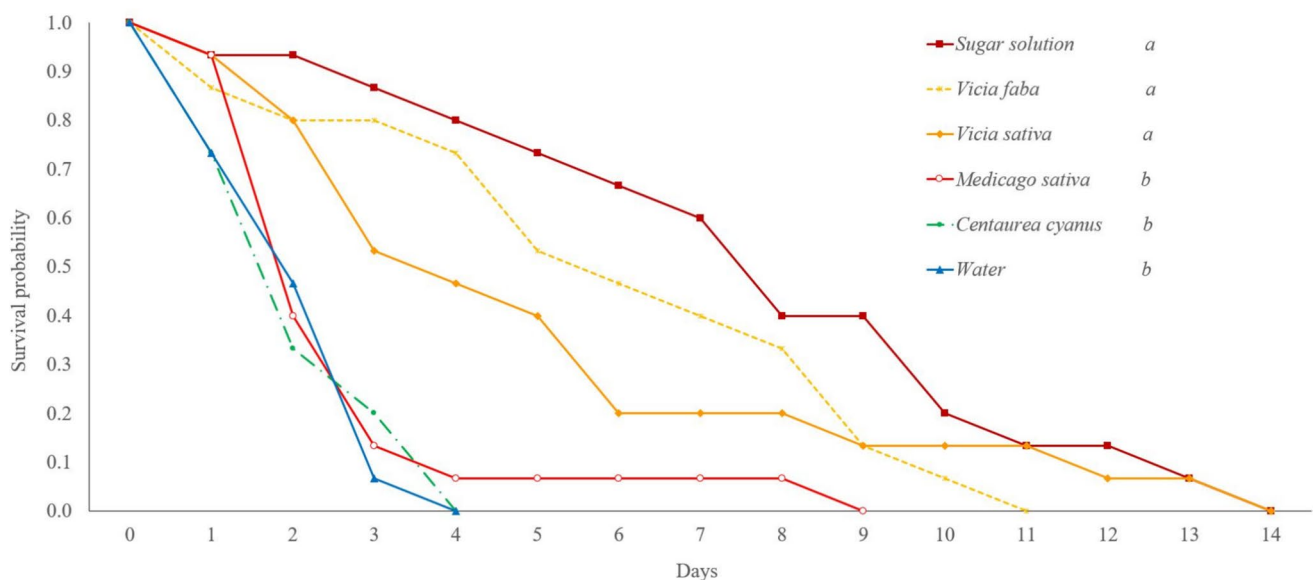
those with access to *E. vesicaria* did not differ significantly from either (*C. officinalis* vs sugar $p=0.2789$, *C. officinalis* vs *E. vesicaria* $p=0.7283$, *E. vesicaria* vs sugar $p=0.8895$, *E. vesicaria* vs *V. faba* $p=0.2342$, *V. faba* vs

sugar $p=0.5229$). Females fed *E. segetalis*, *M. arvensis*, or water had low survival rates (17.5, 10, and 5%, respectively) and were not included in the egg load analysis.

Table 1 Pairwise comparisons of the survival curves of *Aphidoletes aphidimyza* females ($n=16$) (first assay) fed on different floral and extrafloral nectars (*Calendula officinalis*, *Euphorbia segetalis*, *Eruca**vesicaria*, *Moricandia arvensis*, or *Vicia faba*), a 10% sugar solution (glucose, fructose, and sucrose at 1:1:1), or water (log-rank test adjusted using the Benjamini–Hochberg method, $\alpha=0.05$)

Nectar resource	Chi square (X^2) and p value						
	<i>V. faba</i>	<i>E. vesicaria</i>	<i>M. arvensis</i>	<i>E. segetalis</i>	<i>C. officinalis</i>	Sugar solution	Water
<i>V. faba</i>	–	–	–	–	–	–	–
<i>E. vesicaria</i>	1.22 0.3263	–	–	–	–	–	–
<i>M. arvensis</i>	3.17 0.0717	0.45 0.5196	–	–	–	–	–
<i>E. segetalis</i>	4.96 0.0447*	1.25 0.2032	0.20 0.7325	–	–	–	–
<i>C. officinalis</i>	11.81 0.0025*	5.22 0.0016*	2.58 0.0352*	1.34 0.1784	–	–	–
Sugar solution	1.92 0.2968	6.72 0.0090*	10.93 0.0045*	14.32 0.0019*	26.10 <0.0001*	–	–
Water	8.54 0.0065*	3.12 0.0065*	1.19 0.1087	0.41 0.3545	0.27 0.3403	20.80 <0.0001*	–

*Significant differences

**Fig. 5** Kaplan–Maier survival curves for *Aphidoletes aphidimyza* females (second assay) fed on either EFN resources (*Vicia faba*, *V. sativa*, *Medicago sativa*, or *Centaurea cyanus*), a 10% sugar solution (glucose, fructose, and sucrose at 1:1:1), or water under labora-tory conditions (22 ± 1 °C; $80 \pm 2\%$ RH; 16:8 h L:D). Different letters indicate significant differences among food resources based on pairwise comparisons (log-rank test adjusted using the Benjamini–Hochberg method, $\alpha=0.05$)**Table 2** Pairwise comparison of the survival curves of *Aphidoletes aphidimyza* females ($n=15$) (second assay) fed different EFN resources (*Vicia faba*, *V. sativa*, *Medicago sativa*, or *Centaurea**cyanus*), a 10% sugar solution (glucose, fructose, and sucrose at 1:1:1) (positive control), or water (negative control) (log-rank test adjusted using the Benjamini–Hochberg method, $\alpha=0.05$)

Nectar resource	Chi square (X^2) and p value					
	<i>V. faba</i>	<i>V. sativa</i>	<i>M. sativa</i>	<i>C. cyanus</i>	Sugar solution	Water
<i>V. faba</i>	–	–	–	–	–	–
<i>V. sativa</i>	0.03 0.8615	–	–	–	–	–
<i>M. sativa</i>	5.28 0.0055*	4.52 0.0262*	–	–	–	–
<i>C. cyanus</i>	8.23 0.0002*	7.23 0.0040*	0.30 0.6156	–	–	–
Sugar solution	2.05 0.1256	2.70 0.1452	15.69 0.0002*	21.12 <0.0001*	–	–
Water	7.87 0.0002*	6.87 0.0040*	0.23 0.6156	0.01 0.8615	20.53 <0.0001*	–

*Significant differences

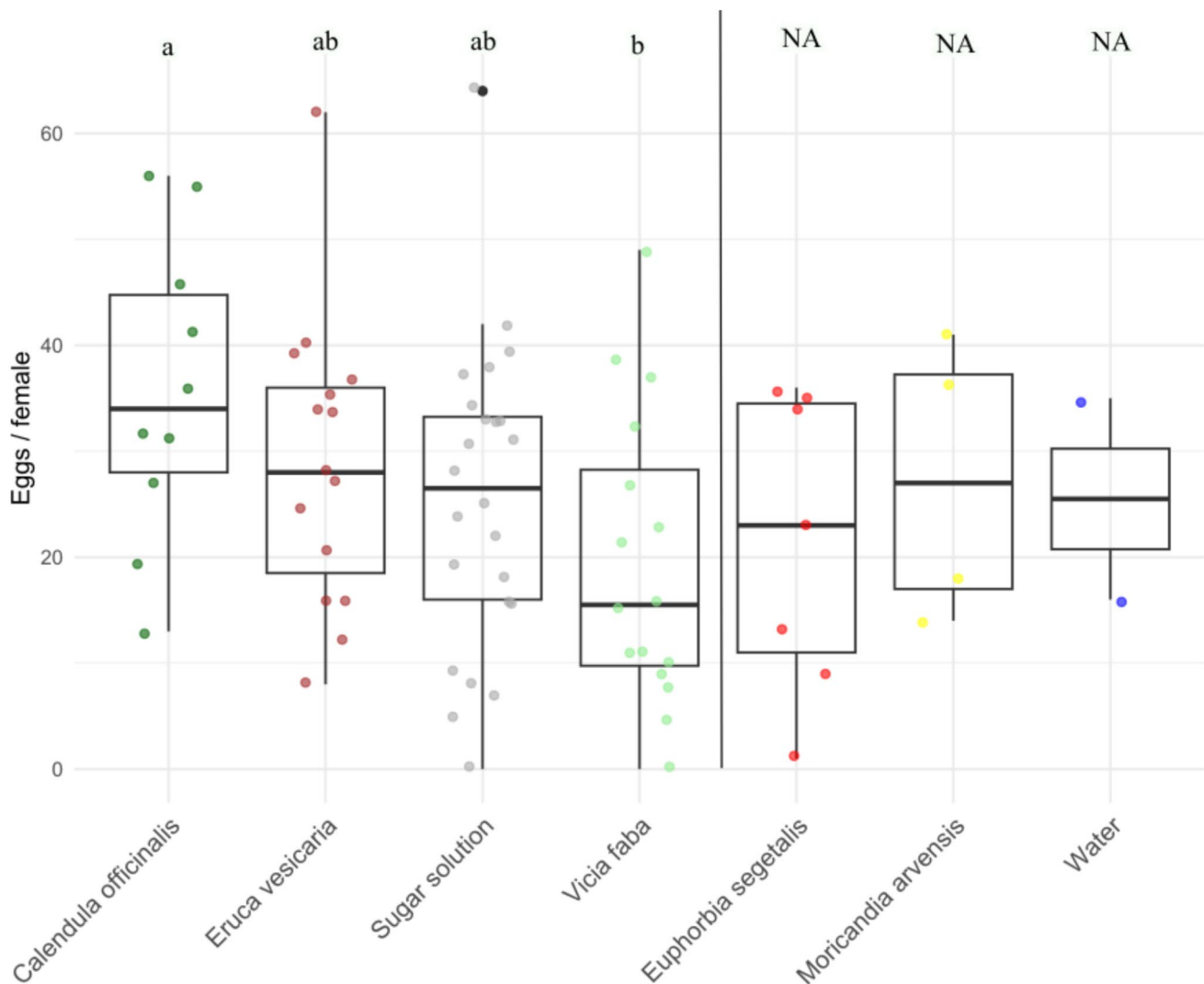


Fig. 6 Egg loads of *Aphidoletes aphidimyza* females (<96 h old) fed on different food resources under laboratory conditions (22 ± 1 °C; $80 \pm 3\%$ RH and 16:8 h L:D); NA = not included in the analysis due to the low number of repetitions

Discussion

This study examines the response of *A. aphidimyza* to potential components of an attract and reward strategy aiming to improve the biological control of aphids by boosting populations of this predator. The present study performed the initial step in this strategy by evaluating attractants and supplementary food sources for adult natural enemies.

Our results show that none of the singly tested HIPVs or plants attracted *A. aphidimyza* females. Therefore, we conclude that these isolated compounds and plant species have no potential as effective attractants in an A&R strategy. In the cases of Pal and MeSA, these findings differ from those of previous studies. Molnár et al. (2018) report that these HIPVs elicit an antenna response in newly emerged *A. aphidimyza* females, although that study provides no evidence

of behavioral activity. Our findings regarding Pal also are not directly comparable to those reported by Watanabe et al. (2016), who find that Pal attracts mated 72 h old *A. aphidimyza* females. The discrepancy between our findings and those of Watanabe et al. (2016) could be due to differences in the females' age (72 h old vs. < 24 h old), nutritional status (sucrose solution vs. water), and/or mating status. Watanabe et al. (2016) also used different light conditions than we did (scotophase vs. photophase, respectively). However, it seems unlikely that this discrepancy is due to different light conditions, since Aparicio et al. (2018) conducted olfactometer tests under the same light conditions used in the present study and observed positive responses to alyssum flowers. It seems more likely this discrepancy between this study and Watanabe et al. (2016), may be attributed to nutritional status, as the nutritional status of the larvae (which probably

differed in our studies) might influence the foraging behavior and thus the movement of young *A. aphidimyza* adults. For example, according to Sell and Kuo-Sell (1987), female egg production during the first two days of life is strongly influenced by the nutritional reserves accumulated during the larval stage.

Although we find that *A. aphidimyza* females exhibit no preference for single compounds, it is still possible that this predator might respond to mixtures including these compounds. This is the case for another dipteran, *Eupeodes volucris* Sacken (Diptera: Syrphidae), which, in another study, did not show attraction to either Pal or MeSA but did show attraction to a quaternary mixture containing both of these HIPVs, 2-phenylethanol, and acetic acid (Jones et al. 2016). In any case, our attraction assay aimed to simulate the conditions of newly emerged females in a less favorable scenario during the beginning of the season, when food resources are scarce. Due to the importance of HIPVs to *A. aphidimyza* oviposition (Higashida et al. 2022) and the practical implications of this predator for biological control, more research is needed to determine whether the age and/or nutritional status of the females influence their attraction to these compounds.

As with the HIPVs, our results indicate that *A. aphidimyza* females are not attracted to the five evaluated plant species, which were drawn from four families: two Brassicaceae, one Asteraceae, one Euphorbiaceae and one Fabaceae. The potential attraction of *A. aphidimyza* adults to flowers has received very little attention in previous literature. Only Aparicio et al. (2018) show that *A. aphidimyza* females are attracted to *L. maritima*, a species belonging to Brassicaceae. This discrepancy in findings regarding the attraction of *A. aphidimyza* females to flowers of different species of Brassicaceae can be attributed to differences in the chemical composition of flower fragrances, as the number and identities of volatiles vary among flower species (Dobson 1994). Other abiotic factors, such as climatic conditions and plant nutrient availability, have also been reported to affect the emission of induced plant volatiles (Gouinguéné and Turlings 2002). In addition, the attraction mediated by nectar can be impacted by microorganisms such as yeasts and bacteria, which may change the volatile profile of nectar and therefore alter the insect's olfactory response (Ermio et al. 2024). Therefore, further research is required to determine whether and how plant volatiles, nectar, or the interactions among plants, microorganisms, and abiotic factors influence the attraction of natural enemies such as *A. aphidimyza* to flowers.

Our study also hypothesized that nectar from flowers or extrafloral nectar would provide *A. aphidimyza* with high-quality food resources. Of the plants tested, *V. faba*, *V. sativa*, and the flowers of *E. vesicaria* enhanced predator survival and thus show promise for use as insectary plants in

crops to improve this predator's performance. Our findings regarding the two *Vicia* species, which have EFN, align with those of Aparicio et al. (2018); these results highlight the importance of nectar availability for *A. aphidimyza*, which may struggle to access hidden nectaries due to the length of its legs. Our study also shows that not all insectary plants with accessible nectar improve the survival of *A. aphidimyza* females, since extrafloral nectaries of *Euphorbia* spp., *M. sativa*, and *C. cyanus* did not enhance *A. aphidimyza* fitness. This result indicates that accessibility is not the only factor impacting insect feeding (Wäckers 2004); factors such as insect morphology, digestive capacity, and gustatory response may also influence optimal utilization of nectar sources (Wäckers 2005).

Our results indicate that *A. aphidimyza* females are synovigenic, since the egg load recorded 96 h after emergence varied a great deal, ranging from zero to 64 eggs per female. This is far from the average lifetime fecundity of 250 eggs per female (Boulanger et al. 2019) and from the approximately 12 mature eggs (authors' unpublished results) that *A. aphidimyza* have just after emergence. The fecundity of young females depends on food resources during larval development (Havelka and Ruzicka 1984), which might also contribute to the variability of egg load in the present study. However, our assay was conducted with females that were fasted for 24–48 h, and this likely reduced the effect of feeding during the larval stage (Sell and Kuo-Sell 1987; Boulanger et al. 2019). Despite the variability of results observed in our study, we find significant differences between the egg loads in females fed *V. faba* and in those fed *C. officinalis*, the two resources leading to the best and worst survival rates, respectively. Similar results have been reported in previous studies of parasitoids. For example, Arnó et al. (2018) determined that the plant *Ononis natrix* L. (Fabaceae) positively impacts the egg load of the parasitoid *Bracon* nr. *nigricans* Szépligeti (Hymenoptera: Braconidae) but has no effect on the survival of adults. Arnó et al. (2018) attribute this effect to the exudates that, according to Wollenweber et al. (2003), cover the plant and can function as a food resource for certain parasitoids (Olson and Nechols 1995). This could also be the case for *C. officinalis*, since Sharma and Kumari (2021) report the presence of 15 free amino acids in the flowers of this species. Overall, our results highlight the importance of plant diversity, since some plant species (*V. faba*, *V. sativa*, and *E. vesicaria*) are promising to increase survival, while others (*C. officinalis*) are promising to boost fecundity in *A. aphidimyza*.

We find that *A. aphidimyza* females do not seem to use Pal or MeSA alone to locate aphid colonies, so more research is needed on the potential use of these volatiles in lures to attract this predator in field conditions. The present study has identified four Mediterranean plant species (*V. faba*, *V. sativa*, *E. vesicaria*, and *C. officinalis*) that do not attract *A. aphidimyza*

but do positively impact its fitness. These findings highlight the possible role of nectar in feeding this predator in the absence of honeydew, as suggested by Aparicio et al. (2018). Therefore, additional studies are needed to identify other plant species that could be promising to enhance the survival and reproduction of this aphid predator. Further research in field conditions is also needed to determine whether these promising plant species that improve *A. aphidimyza* fitness at laboratory conditions also increase their abundance and biological control of aphids, especially at the beginning of the season at field. In early spring, honeydew is scarce or absent, and abundant appropriate plant species during this time could increase female survival, giving the predator more opportunities to locate suitable aphid colonies in which to lay eggs. Although the number of eggs has been found to be independent of food resources just after emergence (Sell and Kuo-Sell 1987), the availability of plant-derived sugary sources would offer benefits by increasing foraging options. As *A. aphidimyza* larvae are furtive predators with very low mobility, adult females must locate suitable colonies capable of supporting offspring development. Therefore, selected plant species may be very useful for increasing the efficacy of *A. aphidimyza* as a biological control agent.

Author contributions

LGM, GA, OA, CQ, SL and JA conceived and designed research. LGM, GA and JA conducted experiments. LGMB, GA, OA, CQ, SL and JA analysis data. LGM wrote the first draft manuscript. All authors read and approved the final version of the manuscript.

Acknowledgements The authors thank Aleix Teruel i Subirats and Pilar Hernández García for their support. This research work was funded by grants PID2019-107030RB-C21 and PID2022-139988OB-I00 funded by MICIU/AEI/<https://doi.org/10.13039/501100011033> and, by ERDF/EU. LGMB is a beneficiary of the grant PRE2020-092229 funded by MICIU/AEI/<https://doi.org/10.13039/501100011033> and, by “ESF Investing in your future”. All IRTA’s authors were also funded by the CERCA Programme / Generalitat de Catalunya.

Funding Open Access funding provided thanks to the CRUE-CSIC agreement with Springer Nature. The authors have not disclosed any funding.

Data availability No datasets were generated or analysed during the current study.

Declarations

Conflict of interest The authors declare no competing interests.

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