



## OPEN Role of eggplant trichome in whitefly oviposition and its relevance to biological control under greenhouse conditions

Estefanía Rodríguez<sup>1</sup>✉, Mario Porcel<sup>2</sup>, Lidia Lara<sup>1</sup>, Tomás Cabello<sup>4</sup>, Manuel Gámez<sup>5</sup>, Leticia Navarro<sup>3</sup>, Alberto Domingo<sup>3</sup>, Francisco Javier Burguillo<sup>6</sup> & María del Mar Téllez<sup>1</sup>

The combined release of the predatory mite *Amblyseius swirskii* (Athias-Henriot) and the mirid *Nesidiocoris tenuis* (Reuter) provides effective biological control of the tobacco whitefly (*Bemisia tabaci* (Gennadius)) in greenhouse eggplant. However, knowing how plants' trichomes affect pest-predator interactions could improve whitefly management. Here, the effect of two varieties with either the presence or absence of trichomes was assessed on naturally occurring whitefly populations and predator abundance in a first experiment under field conditions. Predator-prey models were developed to assess the effect of trichomes on pest and predator population dynamics under field conditions. In a second semi-field experiment, the occurrence and oviposition preferences of *B. tabaci* and *A. swirskii* in the same eggplant varieties were compared. Significantly higher numbers of whitefly and mite, adults and eggs, were found on the hairy variety in both experiments. However, no differences were found in *N. tenuis* abundance between varieties under field conditions. Predator-prey models showed that whitefly growth rate increased in the hairy variety. *N. tenuis* and *A. swirskii* showed different fitness parameters according to the variety, with the former displaying better performance in the hairless variety and the latter in the hairy variety. Both predators effectively controlled the increase in whitefly populations in both varieties. Overall, the findings suggest that the hairless variety is more effective in deterring whiteflies. Additionally, the higher population of *A. swirskii* on the hairy variety indicates that this predator benefited from both the presence of trichomes and the prey.

**Keywords** Antixenosis, Aubergine, Brinjal, Integrated pest management, Leaf trichomes, Non-glandular trichomes

Trichomes give plants their characteristic pubescent or hairy texture, making them undesirable or unattractive for oviposition or feeding by some phytophagous insect species<sup>1,2</sup>. Trichomes may also complement the plant's chemical defenses by possessing glands (glandular trichomes) that exude allelochemicals that act as insect olfactory or gustatory repellents<sup>3,4</sup>. Generally speaking, trichomes are involved in direct plant defenses against insect attacks, either by physical hindrance or by secreting toxic or behaviour-modifying chemicals. Therefore, trichomes have been used to develop insect-resistance varieties in many important crops such as alfalfa, soybean, chickpea, cotton, sorghum, potato, and tomato<sup>1,2</sup>. On the other hand, some generalist and specialist herbivore insects can avoid trichome-based plant defenses to the detriment of the plant<sup>5,6</sup>. Some insect species perform better on plants with trichomes, and trichomes' positive effect in enhancing insect locomotion has been described. For instance, long-legged Hemiptera such as *Nezara viridula* (L.) (Hemiptera: Pentatomidae), tend to be less deterred by glandular stellate trichomes of eggplant<sup>7</sup>. The predatory mirid *Dicyphus errans* (Wolff) lives on a range of pubescent plant species<sup>8</sup> as well as *Pameridea roridulae* that survives on sticky plants<sup>9</sup>. In some cases, the records reveal that trichomes have more harmful than beneficial effects on predators<sup>10</sup>. However, trichomes are preferred oviposition sites for phytoseiid mites and offer refuge (or domatia), retaining and benefiting predatory mites on the plant<sup>11,12</sup>. Hence, the type and density of trichomes may play a crucial role

<sup>1</sup>Department of Sustainable Crop Protection, IFAPA, La Mojonera- Centre, Almería, Spain. <sup>2</sup>Department of Sustainable Crop Protection, IFAPA, Churriana-Centre, Málaga, Spain. <sup>3</sup>Rijk Zwaan Iberica SA, Almería, Spain.

<sup>4</sup>Department of Biology and Geology, University of Almeria, Almería, Spain. <sup>5</sup>Department of Mathematics, University of Almería, Almería, Spain. <sup>6</sup>Department of Physical Chemistry, University of Salamanca, Salamanca, Spain. ✉email: mestefania.rodriguez@juntadeandalucia.es

in explaining the specific host-plant associations, adaptations, and herbivory patterns of certain phytophagous insects and their natural enemies<sup>13</sup>. Therefore, trichomes serve as suitable characters for manipulation in these interactions, presenting an opportunity for pest control strategies through breeding programmes.

Eggplant (*Solanum melongena* L.) is a significant solanaceous crop in tropical and temperate parts of the world. In Europe, the province of Almería (Andalusia, SE Spain) is the third-largest producer and the leading supplier for the Northern European market, producing 220,897 metric tons/year of eggplants grown over 2,387 Ha of greenhouses<sup>14</sup>. The tobacco whitefly, *Bemisia tabaci* (Gennadius) (Hemiptera: Aleyrodidae), is one of the most prominent agricultural pest and plant virus vector in Europe<sup>15</sup>. The host plant preference and fitness parameters shown on eggplant by the tobacco whitefly make it the most damaging pest to this crop's greenhouse production<sup>16,17</sup>. Besides *B. tabaci*'s rising resistance to common pesticides<sup>18–20</sup>, excessive pesticide use poses significant risks to both the environment and human health<sup>21</sup>. In the Almería greenhouse production area, the tobacco whitefly is commonly controlled using Integrated Pest Management (IPM), an environmentally friendly approach based on commercial biological control applied to approximately 60% of the cultivated eggplant surface<sup>14</sup>. Control is mainly achieved through the inoculative release of the predatory mite, *Amblyseius swirskii* (Athias-Henriot) (Acari: Phytoseiidae), and complementary, of the mirid *Nesidiocoris tenuis* (Hemiptera, Miridae). In general, *A. swirskii* is known as pollen-feeding generalist predator<sup>22</sup>. In addition, some species of phytoseiid predators can also feed on and survive on the plant sap of some plant species without causing economic damage, when its primary prey are absent<sup>23,24</sup>. *N. tenuis* is a zoophytophagous insect that can feed on cultivated plants when prey is scarce<sup>25–27</sup>. Both predators mainly prey on whitefly eggs and nymphal stages rather than on adults<sup>26,28,29</sup>. Therefore, pest control in eggplant production remains challenging due to whitefly adults coming into greenhouses from the outdoor environment and colonizing the crop.

For IPM of agricultural crop pests, the use of tolerant varieties of host plants is a tactic that can effectively reduce crop damage and pesticide application<sup>30</sup>. Trichomes are a common feature of vegetative and reproductive structures in many plant species that have been used to develop insect resistance varieties in several crops<sup>2</sup>. Notably, the role of trichomes on the food preferences of *B. tabaci* and host suitability among different eggplant varieties has been addressed. Whitefly susceptibility is generally higher in varieties with greater trichome density<sup>31–34</sup>. However, no research has focused on the effect of trichomes on whitefly predator interactions on eggplant under field conditions and from a pest management perspective. Greater knowledge of the population dynamics of the pest and its predators on different eggplant varieties with the presence or absence of trichomes would lead to a better interpretation of the predator-prey interactions in the field and improve biocontrol strategies. For instance, employing eggplant varieties more susceptible to whitefly as trap crops<sup>35</sup>, or utilizing varieties conducive to the establishment of natural enemies<sup>36</sup>.

In this study, the variations in whitefly attraction and egg-laying behavior, as well as the abundance of the two whitefly predators, the mite *Amblyseius swirskii* and the mirid *Nesidiocoris tenuis*, between two eggplant varieties that differed in the presence of plant trichomes were examined in a first experiment under field conditions. Predator-prey models were developed to describe population dynamics with a view on selecting the best variety for whitefly control under field conditions. In a second semi-field experiment, the occurrence and oviposition preferences both the pest *B. tabaci* and the predatory mite *A. swirskii* in relation to the presence or absence of trichomes was evaluated.

## Results

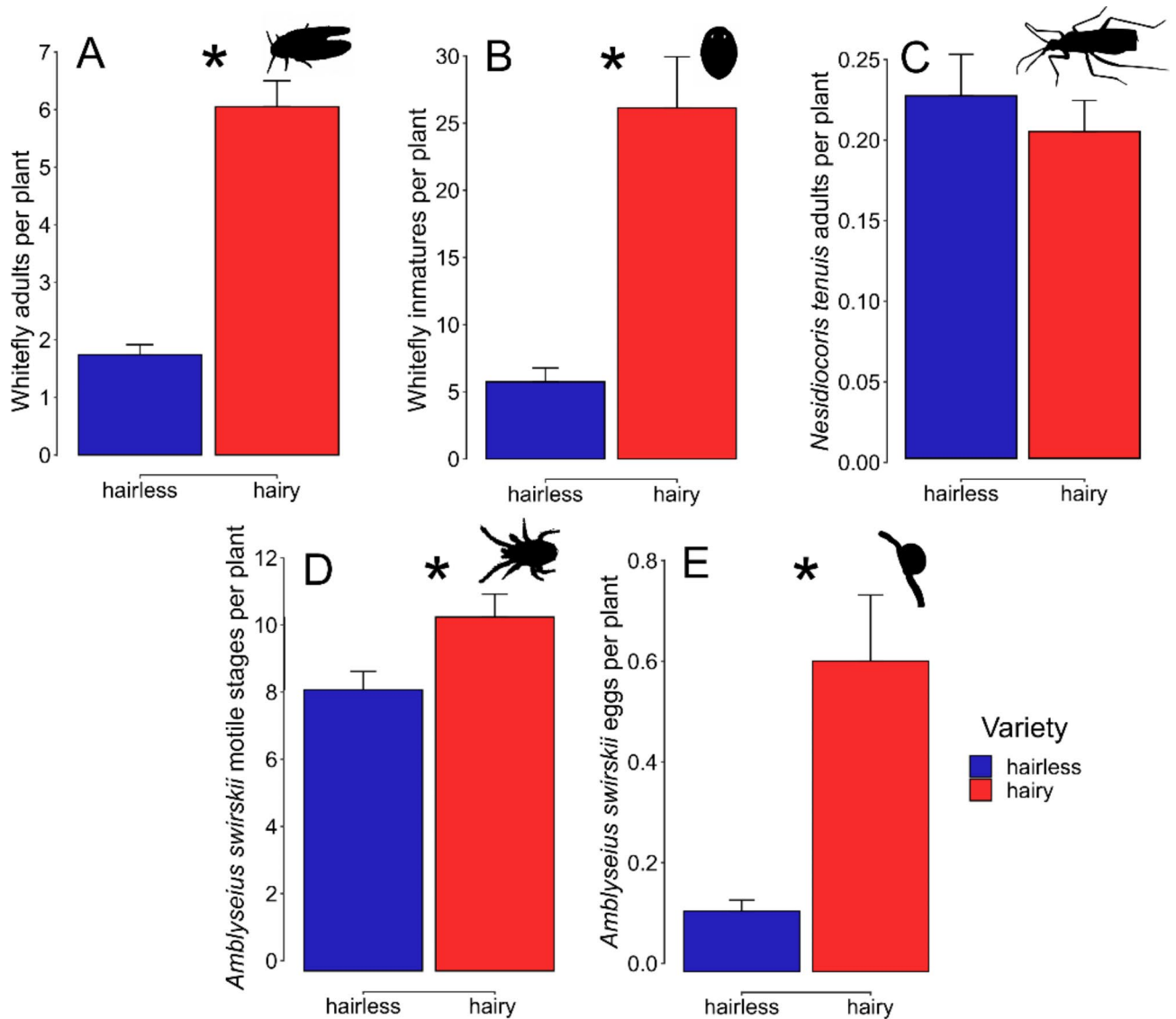
### Whitefly and predators' abundance in field conditions

The abundance of adult and immature stages of whiteflies was significantly higher in the hairy than in the hairless variety (Fig. 1). Similarly, motile stages and eggs of *A. swirskii* were significantly more abundant in the hairy than in the hairless variety (Fig. 1). No statistically significant differences were observed in *N. tenuis* abundance between varieties (Fig. 1). Block significantly affected the immature stages and adult whiteflies as well as the egg abundance of *A. swirskii* (see block effects in Table 1). However, block had no significant effect on the abundance of motile stages of *A. swirskii* or *N. tenuis* (Table 1).

### Predator-prey models

The  $R^2$  value expressed that the two models corresponding to the two eggplant varieties were statistically well-fitted for density variables (insect/day) (Table 2). The  $R^2$  value in the hairless variety was 0.98 (d.f.=12,  $P < 0.010$ ), and 0.84 (d.f.=12,  $P < 0.010$ ) in the hairy variety, indicating the significant prediction of both models (Table 2). The whitefly growth rate ( $r_{m1}$ ) was similar in both varieties (Table 2). However, the whitefly population dynamics over time resulted in two pest outbreaks in the hairy variety (reaching more than 500 insect/day), while the hairless model outcome displayed a single outbreak with a value of less than 200 insect/day (Fig. 2). These results indicate the suitability of the hairy variety for whitefly. The *A. swirskii* mortality rate ( $m_2$ ) was slightly higher in the hairless variety (Table 2), suggesting better suitability of the hairy variety for this predator.

In contrast, the *N. tenuis* mortality rate ( $m_2$ ) was twice as high in the hairy variety as compared to the hairless variety, indicating that in the absence of prey, a lack of trichomes reduces *N. tenuis* mortality. Similarly, the predation rate was much greater for *N. tenuis* in the hairless variety and greater in the hairy variety for *A. swirskii* (Table 2). Therefore, *N. tenuis* and *A. swirskii* showed different fitness parameters according to the variety, with the former displaying better performance in the hairless variety and the latter in the hairy variety. Consequently, the benefit rate ( $c_1$  and  $c_2$ ) was different for both predators (Table 2). Finally, regarding pest control, models showed that both predators controlled the increase in whitefly population in both varieties and eventually suppressed it (Fig. 2).



**Fig. 1.** (A) Whitefly adults, (B) whitefly immature stages, (C) *N. tenuis* (adults and nymphs), (D) *A. swirskii* motile stages and (E) *A. swirskii* eggs recorded per plant in the hairless and hairy variety of eggplant in the field experiment. Asterisks indicate statistically significant differences between varieties (GLMM, Wald test,  $P < 0.001$ ).

### Whitefly and mite' abundance in semi-field experiment

The abundance of immature stages of whiteflies was significantly higher in the hairy than in the hairless variety ( $\chi^2 = 74.7$ , d.f. = 1,  $P < 0.001$ ) (Fig. 3). Similarly, motile stages and eggs of *A. swirskii* were significantly more abundant in the hairy than in the hairless variety ( $\chi^2 = 94.2$ , d.f. = 1,  $P < 0.001$ ) ( $\chi^2 = 65.7$ , d.f. = 1,  $P < 0.001$ ) (Fig. 3).

### Discussion

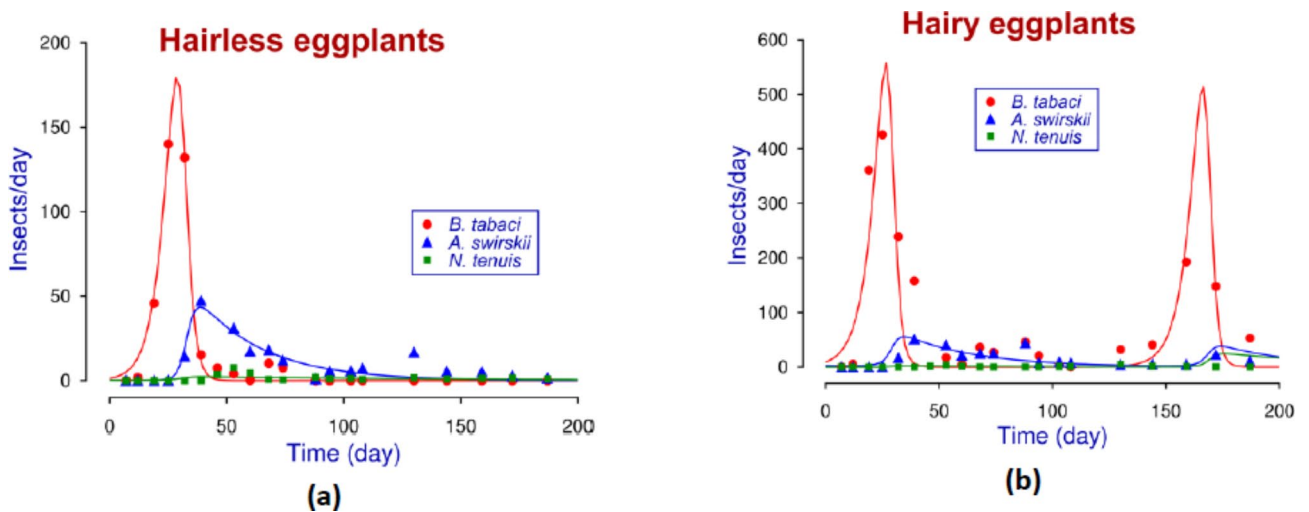
The abundance of whiteflies was significantly higher on the variety with trichomes, which also had a significantly higher abundance of immature stages. These results were consistent across both the field experiment, where predators were present, and the semi-field experiment, where predators were absent. In a field experiment, a significant effect of the block on whitefly adult and immature stages was also found, suggesting that there were different environmental conditions between blocks. Regarding predator-prey models, our results demonstrated that the variety possessing trichomes was more susceptible (higher growth rate) to whitefly, and also displayed a higher frequency and magnitude of pest outbreaks compared to the hairless variety. Combined, our results support that *B. tabaci* significantly prefers trichomes, which also favors pest oviposition. The density and type of trichomes (non-glandular) could be a probable reason for the results found for *B. tabaci*. For instance, a higher trichome density is related to the colonization and oviposition preference of *B. tabaci* in cotton varieties<sup>37,38</sup>. In tomato varieties, glandular trichome density is negatively correlated with whitefly attractiveness and oviposition, while non-glandular trichomes density is positively correlated with whitefly oviposition<sup>4,39</sup>. In eggplant varieties,

Species	Model	Type	Fixed factors	Estimate	SE	d.f	$\chi^2$	p-value
<i>B. tabaci</i>	Adults	GLMM	Variety	1.46	0.11	1	172.7	<0.001
			Block	0.23	0.11	1	4.8	0.0286
	Immatures	GLMM	Variety	2.86	0.24	1	147.8	<0.001
			Block	1.13	0.21	1	28.3	<0.001
<i>A. swirskii</i>	Motile stages	ZIGLMM	Variety	0.34	0.07	1	20.1	<0.001
			Block	0.04	0.08	1	0.3	0.572
	Eggs	GLMM	Variety	1.71	0.29	1	35.5	<0.001
			Block	1.00	0.27	1	13.4	<0.001
<i>N. tenuis</i>	Adults and nymphs	GLMM	Variety	0.12	0.20	1	0.3	0.558
			Block	0.22	0.20	1	1.2	0.268

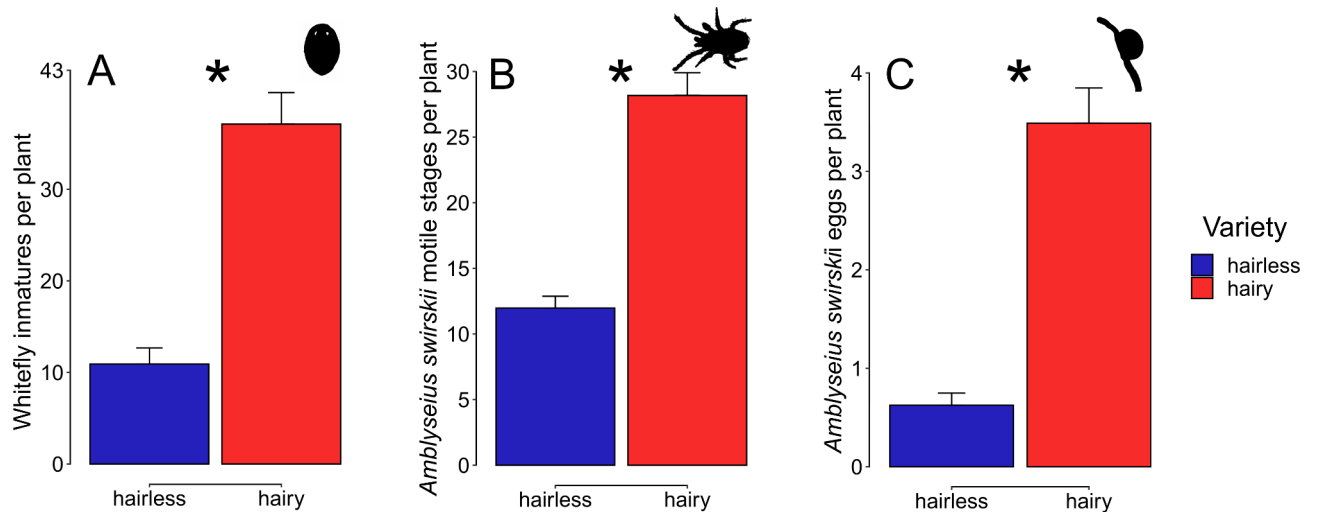
**Table 1.** Results of the generalized linear mixed models used to analyse the field experiment datasets comparing the abundance of *B. tabaci*, *A. swirskii* and *N. tenuis* on hairy and hairless eggplant varieties. *B. tabaci* immature include eggs and nymphs. *A. swirskii* motile stages include adults and immature stages. GLMM Generalized linear mixed model, ZIGLMM zero-inflated generalized linear mixed model.

Variety	Fitting parameters (average $\pm$ SE)						
	$r_{m1}$	$m_2$	$m_3$	$\gamma_{12}$	$\gamma_{13}$	$c_1$	$c_2$
Hairless	0.2697	0.0349	0.009	0.002	0.2564	1.421	0.004
	$\pm 2.33 \cdot 10^{-3}$	$\pm 6.03 \cdot 10^{-3}$	$\pm 1.09 \cdot 10^{-3}$	$\pm 2.38 \cdot 10^{-4}$	$\pm 7.53 \cdot 10^{-2}$	$\pm 1.47 \cdot 10^{-4}$	$\pm 1.57 \cdot 10^{-4}$
	d.f. = 12; $R^2 = 0.9771$ ; $P < 0.01$						
Hairy	0.2008	0.0309	0.018	0.012	0.0099	0.05	0.0077
	$\pm 6.63 \cdot 10^{-3}$	$\pm 8.33 \cdot 10^{-3}$	$\pm 1.45 \cdot 10^{-2}$	$\pm 3.01 \cdot 10^{-3}$	$\pm 3.09 \cdot 10^{-2}$	$\pm 1.10 \cdot 10^{-6}$	$\pm 5.67 \cdot 10^{-5}$
	d.f. = 12; $R^2 = 0.8433$ ; $P < 0.01$						

**Table 2.** Fitting and statistical parameters of the one-prey two predator models for the two eggplant varieties (hairless and hairy) under greenhouse field conditions. Prey is the tobacco whitefly *Bemisia tabaci*, and the two predators are the mite *Amblyseius swirskii* and the mirid *Nesidiocoris tenuis* ( $r_{m1}$  is per capita growth rate of the prey species (P),  $m_2$  and  $m_3$  are the mortality rate of predator  $E_1$  and predator  $E_2$ , respectively).



**Fig. 2.** Densities obtained from the two fitted models: prey species = *Bemisia tabaci* (egg and nymph stages), predator species = *Amblyseius swirskii* (eggs and motile stages) and *Nesidiocoris tenuis* (adults and nymphs), in greenhouse eggplant crop for the hairless (A) and hairy (B) varieties. Figures have a different scale for the y-axis to facilitate visualization of dynamic populations predators on hairless variety.



**Fig. 3.** (A) Whitefly immature stages, (B) *A. swirskii* motile stages, and (C) *A. swirskii* eggs recorded per plant in the hairless and hairy varieties of eggplant in the semi-field experiments. Asterisks indicate statistically significant differences between varieties (GLMM, Wald test,  $P < 0.001$ ).

only a wild variety that bore a higher density of glandular trichomes harbored the lowest whitefly population<sup>34</sup>. Wild species of eggplants bear different types of glandular trichomes, while cultivated species usually bear branched stellate trichomes (non-glandular)<sup>40</sup>. It has been well documented that cultivated hairy leaf varieties are associated with higher *Bemisia* populations compared with glabrous leaf varieties in eggplant<sup>31–33</sup>. Among other morphological leaf characteristics, trichome density positively correlated with the number of whitefly adults and eggs in eggplant varieties bearing trichomes<sup>34</sup>. The last agrees with our finding that invading whitefly adults in greenhouses coming from outdoor environments chose preferentially to reproduce on the hairy variety. Similar results have also been found in other crops, such as cucumber<sup>41,42</sup> and cotton<sup>43</sup>. In cotton, trichome density was positively related to *Bemisia*, but adult densities decreased when trichome density became too high, affecting *Bemisia* activity<sup>44,45</sup>. The reasons why hairy leaf varieties harbor higher whitefly populations could be related to the preference of whitefly to oviposit near trichomes, protecting their eggs from predators and parasitoids<sup>46,47</sup>, or improving the microhabitat<sup>48</sup>. Cotton leaves with more trichomes create an adequate microhabitat for oviposition and development of *B. tabaci*<sup>49</sup>. Leaf hairiness increases humidity on leaf surfaces<sup>50</sup>, which can be significant under hot and dry climatic conditions because low humidity may affect the survivorship of eggs and first instar nymphs, which can become dehydrated<sup>51,52</sup>. For *B. tabaci*, selecting a host plant is crucial to favor nymphal development due to the sessile nature of their nymphal stages<sup>16</sup>. From an applied point of view, the hairy variety, the most suitable for *B. tabaci*, could be used by growers to attract the pest away from the crop improving whitefly control. This technique, known as trap cropping, can reduce crop damage and the need for conventional pesticide applications<sup>53</sup>. On the other hand, hairless varieties with a high level of non-preference can also be used by plant breeders as a source of resistance against *B. tabaci* in plant breeding programs.

Similarly, trichomes had a significant positive effect on the abundance of the predatory mite *Amblyseius swirskii*. Interestingly, this positive effect of trichomes on *A. swirskii* was observed even in the semi-field experiment and in the absence of prey. Under field conditions, as expected for a controlled release, a significant effect of the block on *A. swirskii* abundance was not found, however, it affected egg abundance. These results suggest that, over time, environmental and ecological conditions between blocks affected the oviposition preferences of *A. swirskii*. Predator-prey models showed lower mortality and higher predation rate of *A. swirskii* on the hairy variety. Combined our results suggest that *A. swirskii* benefited from both the presence of trichome and the prey on the hairy variety. Trichome density is a vital plant characteristic for phytoseiid mites<sup>11,12</sup>. Increasing trichome density can lead to decreased walking speed, increased time to predation, and lower predation rate. However, leaves with non glandular trichomes or leaf domatia are often inhabited by large populations of predatory mites<sup>11,12</sup>. Pepper plants with domatia used as banker plants support (A) *swirskii* populations in greenhouse crops<sup>12</sup> and significantly reduce (B) *tabaci*<sup>54</sup>. *Amblyseius swirskii* is a predator specifically released for controlling both thrips and whiteflies<sup>29,55</sup>, but it is very effective for reducing whitefly population, even in greenhouse crops through cold seasons as in this study<sup>56</sup>. The combination of the presence of trichomes and suitable prey (whitefly) probably resulted in increased populations of this predatory mite in the hairy variety. As mentioned above, trichome-bearing varieties exhibit a higher relative humidity within the microclimate on the leaves. This is also beneficial for the development and population increase of *A. swirskii*<sup>57</sup>.

Finally, opposite results were found for the zoophytophagous mirid *N. tenuis*. Although we did not find statistical differences in *N. tenuis* abundance between varieties were not observed, predator-pest models showed that the mortality and predation rates increased in the hairy variety, indicating a better performance of the mirid in the glabrous variety. This result differs from what was observed for glandular trichomes in the case of *N. tenuis* and other mirids such as *D. errans* and *P. roridulae*. These mirids seem to prefer sticky plants with glandular trichomes on which *N. tenuis* is perfectly adapted to move and actively hunt for prey<sup>8,9,58</sup>.

Predator-pest models showed that predators effectively controlled the increased whitefly population in the hairless variety as well, underscoring their efficacy in pest control even in the absence of trichomes. Mathematical models can help to understand better systems in addition to experimental data<sup>59,60</sup>. Compared to open fields, ecosystems within greenhouses are relatively simplified<sup>61</sup>, enabling more controlled ecological studies and, thereby, facilitating predator-prey development models with several species<sup>62</sup>. From a biological control perspective, the Verhulst-Pearl and Lotka-Volterra logistic functions for the predator-prey system, and the Nicholson and Bailey model for the host-parasitoid system, are among the most widely used to study the population dynamics of pests with their natural enemies<sup>63</sup>. Use of these functions has clarified, simulated, and/or predicted effects of decisive factors in biological control inclusion in Integrated Pest Management (IPM) programs in greenhouses such as the prey/host or predator/parasitoid ratio, initial density, release rate, timing, and the selection of control agents<sup>56,62,64–67</sup>.

## Conclusions

The hairless variety of eggplant was identified as an effective deterrent to *B. tabaci*. The absence of trichomes didn't necessarily result in a complete absence of the pest, but rather a reduction. While this hairless variety may indeed have been less favorable for predatory mite development, it didn't hinder its establishment, as the study's population dynamics models demonstrate, ultimately allowing for efficient whitefly control in the field. Combining hairless varieties with appropriate mite dosage rates and/or utilizing trichome-bearing plants as 'trap crops' could lead to a more sustainable pest control strategy and a decrease in insecticide usage.

## Methods

### Study site and experimental design in field conditions

Two eggplant varieties typically cultivated in warm, southern climatic conditions were used to determine the influence of trichomes on the abundance and population dynamics of whiteflies and their predators. Two varieties were employed, differing in trichome density: (i) Thelma<sup>\*</sup>, a standard commercial variety characterized by trichomes (hairy variety), and (ii) Kesia<sup>\*</sup>, a variety nearly devoid of trichomes (hairless variety). The study was conducted throughout the eggplant growing cycle, starting in early September 2019 and concluding in early March 2020 (18 weeks), at a commercial greenhouse spanning approximately 3,000 m<sup>2</sup> (140 m × 22 m) in Almería, Spain (latitude 36° 47' 21''N, longitude 2° 44' 10''W). The average temperature and relative humidity during the experiment were 17.6 °C ± 5.5 SD and 69.9% ± 7.9 SD. Rijk Zwaan Iberica S.L. supplied both varieties. The experimental design was a randomized complete block with two blocks (1,500 m<sup>2</sup>) separated by a plastic mesh, and two plots in each block. The treatments involved randomly applying both varieties (Thelma<sup>\*</sup> and Kesia<sup>\*</sup>) in each block. There were two unplanted rows between the plots. Each plot was eight rows wide and 12.2 m long, with rows spaced 0.5 m apart.

### Whitefly and predator abundance assessment in field conditions

The field experiment was conducted in a commercial greenhouse with natural infestations of *B. tabaci* biotype Q (Mediterranean, MED-Q1)<sup>68</sup> and commercial introductions of predators. The natural occurrence of whitefly populations was monitored weekly for 18 weeks. The initial whitefly population, measured as the mean number of whitefly immature stages (eggs + nymphs) prior to predator release, was 33.6 ± 12.6 for the hairless variety and 176.6 ± 79.0 for the hairy variety. *Amblyseius swirskii* and *N. tenuis* were supplied by Biosur<sup>\*</sup> in commercial sachets and plastic bottles, respectively, and released in commercial doses for whitefly control in greenhouse eggplant production in the study area. One sachet of *Amblyseius swirskii* mites per plant (doses of 250 individuals/m<sup>2</sup>) was hung at an average height on the plant. Each sachet is equipped with water-repellent walls and an outlet opening. Inside, a mixture of wheat bran and either sawdust or vermiculite serves as a carrier medium and food for the factitious prey, *Carpoglyphus lactis* (L.) (Acari: Carpocephidae). *Carpoglyphus lactis*, in turn, acts as the food source for *A. swirskii*, ensuring its development until it naturally exits into the crop. The predator-to-prey ratio should ideally range between 1:7 to 1:12<sup>69</sup>. *N. tenuis* was released at doses of 1.5 individuals/m<sup>2</sup>. Predators were released in week 3, and their abundance was monitored weekly for 15 weeks. Each week, ten plants were randomly selected from each plot for inspection to monitor the pest and predators, following a zig-zag route inside the greenhouse. To monitor whitefly immature stages (eggs and nymphs) and *A. swirskii* (eggs and motile stages), ten leaves per plot were removed from the inner part of each plot, taken from the middle section of the plants. These leaves were subsequently assessed in the laboratory using a stereomicroscope (Zeiss Stemi 2000-C, Carl Zeiss Germany). To monitor *N. tenuis* (adults and nymphs) and whitefly adults, six leaves per plant were selected and inspected from all parts of the plant (upper, middle, lower). The numbers of whitefly adults and *N. tenuis* (adults and nymphs) were recorded during this inspection. Collection of plant material, complied with relevant institutional, national, and international guidelines and legislation.

### Semi-field experiments

Two consecutive experiments were conducted at the Centre IFAPA La Mojonera in Almería, Spain, spanning from April 20th to May 17th, and then from May 18th to June 8th, 2022. The experiments utilized twelve walk-in cages measuring W2 x D3 x H2 meters, each equipped with thrips-proof mesh (300 × 300 μm<sup>2</sup>) and individual meshed openings at the front.

In the first experiment, the aim was to determine the occurrence and oviposition preferences of the pest *B. tabaci* in relation to the presence or absence of trichomes using the eggplant varieties Thelma<sup>\*</sup> and Kesia<sup>\*</sup>. In the second experiment, the objective was to assess the impact of trichomes on occurrence and oviposition preferences of the predatory mite *A. swirskii* (fed on pollen) using the same eggplant varieties.

Since no statistical differences were observed concerning the mirid *N. tenuis* under field conditions, only the pest and the mite *A. swirskii* were evaluated under semi-field conditions. Ten potted eggplants, five of each variety, 40 days old and 30–35 cm tall, were placed inside each greenhouse. Plants were watered and fertilized using drip irrigation as needed. No pesticides or fungicides were applied during the experiments.

In the first experiment, seven days after transplanting, all plants were inoculated with ten adult whiteflies of biotype Q (Mediterranean, MED-Q1)<sup>68</sup> from colonies maintained on eggplant plants (cv. Cristal, Fitó) in insect-proof cages under controlled rearing conditions at IFAPA Centre La Mojonera in Almería Spain, with a temperature of  $25 \pm 3$  °C and a photoperiod of 16:8 h light/dark. In the second experiment, seven days after transplanting, each plant was inoculated with one sachet of *A. swirskii* (doses of 250 individuals/m<sup>2</sup>) and was provided with pollen (*Typha latifolia* L.) (Nutrimite™, Biobest SB) dusted over the leaves as a food source.

Each week, 3 leaves from the upper, middle and bottom part of each plant were taken, and all the present, nymphs and egg of *B. tabaci* as well as mobile stages and eggs of *A. swirskii* were counted in the laboratory, using a stereomicroscope (Zeiss Stemi 2000-C, Carl Zeiss Germany). Both semi-field experiments lasted 3 weeks.

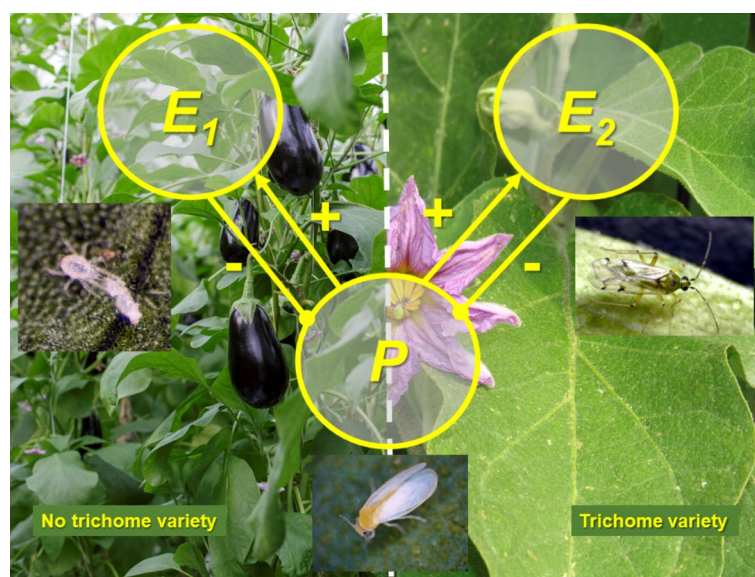
### Statistical analysis

For the field experiment, pest and predator abundance data were analyzed using generalized linear mixed models (GLMM) with the 'glmmTMB' package<sup>70</sup> in R 4.2.2 for Windows. Five models were constructed with the number per plant of whitefly adults, immature stages, *A. swirskii* motile stages, *A. swirskii* eggs, and *N. tenuis* (adults + nymphs) as response variables (Table 1). In the models, eggplant variety and block were set as fixed factors and sampling date as a normally-distributed random effect. A negative binomial distribution with a log-link was used to account for overdispersion. Initially, all models included a zero-inflation term applied to all observations to correct for potential zero-inflation. The inclusion or exclusion of the zero-inflation term in the final model was determined by comparing models with and without the term using the Akaike Information Criterion (AIC) with a cutoff of greater than 2. The semi-field experiment data were analyzed using three GLMMs: one for whitefly immature stages (eggs and nymphs) and the remaining two for *A. swirskii* eggs and motile stages. The models were built with a negative binomial distribution and a log-link and included eggplant variety as fixed factor and block as a normally-distributed random effect. To validate all models, residuals were plotted against the fitted values and each of the fixed effects<sup>71</sup>. Final models were tested for overdispersion and zero-inflation using the simulated scaled residuals with the DHARMA package<sup>72</sup>.

### Predator-pest models

Two predator-prey models were developed, one for each variety, to assess the population dynamics of the whitefly and its predators in field conditions. These models aimed to establish the impact of the presence or absence of eggplant trichomes on pest-predator interactions under field conditions (Fig. 4). The numbers of the whitefly and predators used in the models were expressed as insect-day values (ID). This index, proposed by Ruppel<sup>73</sup>, is used to represent the total impact of pests over a given period and has been previously used to evaluate the effect of biological pest control in horticulture<sup>25,56,64</sup>. ID was calculated using the equation  $[(X_{i+1} - X_i)/2] * (D_{i+1} - D_i)$ , where  $X_i$  and  $X_{i+1}$  are the insect densities (whiteflies or predatory species) in two successive weeks ( $D_i$  and  $D_{i+1}$ ) in days.

Although intraguild predation (IGP) among predators is widespread and associated with natural enemies used in greenhouse production systems<sup>74</sup>, models did not consider the interaction between *N. tenuis* and *A.*



**Fig. 4.** Interaction network. (source competition) considered in the mathematical model, the linking arrows and clubs show benefits (+) and losses (-). Predatory species:  $E_1 = A. swirskii$  and  $E_2 = N. tenuis$ ; prey species:  $P = B. tabaci$  (According to the nomenclature of Mills 2006) on two varieties (trichomes or no-trichomes).

*swirskii*. In practice, results are diverse and the potential risk of intraguild predation disrupting biological control appears to be low in many cases<sup>36,74</sup>. Although both predators are involved in bidirectional IGP, a more complex habitat structure in field settings can reduce the likelihood of IGP<sup>74</sup>. This has been checked in the specific case of *N. tenuis* and *A. swirskii* in pepper plants where it seems that IGP can be neutralized under greenhouse field conditions due to prey variability and food provided by the plant<sup>75</sup>.

Among the non-stage-structured multispecies models, in a first approach, the simplest classical Lotka-Volterra model was applied, where each single-species dynamics exhibit Malthusian growth, indicating an increase in prey populations and decrease in predators. A more precise model would be obtained with logistics rather than Malthusian dynamics<sup>76</sup>. However, in this instance, predator-prey interaction was just proportional to the product of densities, as in the original Lotka-Volterra model.

The network interactions used in our model according to the nomenclature used by Mills<sup>63</sup>, whose equations are shown below:

$$\begin{aligned} \text{Prey (} B. \text{ tabaci)} : \quad & x_1' = x_1(r_{m1} - \gamma_{12} \cdot x_2 - \gamma_{13} \cdot x_3) \\ \text{Predator 1 (} A. \text{ swirskii)} : \quad & x_2' = x_2(-m_2 + c_1\gamma_{12} \cdot x_1) \\ \text{Predator 2 (} N. \text{ tenuis)} : \quad & x_3' = x_3(-m_3 + c_2\gamma_{13} \cdot x_1) \end{aligned} \quad (1)$$

Where  $x_1$ ,  $x_2$  and  $x_3$  are the densities (number/leaf) of pests and predator species, respectively. According to the terminology of Abrams<sup>77</sup>,  $r_{m1}$  is the growth rate of the pest;  $m_2$  and  $m_3$  are the mortality rate of predator 1 and predator 2;  $\gamma_{12}$  and  $\gamma_{13}$  are the slopes of the predator's functional response to killing the pest species by predator 1 and predator 2, respectively;  $c_1$  and  $c_2$  are the coefficients that determine the beneficial rates of prey predation by predators 1 and 2 respectively. The statistical software SIMFIT version 2017<sup>78</sup> was employed to fit the system of Eq. (1) to the data corresponding to the number of leaves. SIMFIT specializes in curve fitting programs, and it includes a program called DEQSOL for fitting experimental data to differential equations. For the integration method of the differential equations, a BDF algorithm with a numerically estimated Jacobian was employed<sup>56,67,78</sup>.

## Data availability

The data that support the findings of this study are available from the corresponding author, [ER] and the second author [MP], upon reasonable request.

Received: 11 September 2023; Accepted: 16 September 2024

Published online: 30 September 2024

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## Acknowledgements

This research was funded by the collaboration agreement (Expediente IFAPA 138/2019) and the European Agricultural Fund for Rural Development (EAFRD) and the National Rural Development Programme (NRDP), and the projects PP.AVA.AVA2019.015 and PP.AVA23.INV2023.028 from the EU-FEDER program. Authors would like to thank Jose A. Viñolo Castillo for kindly permitting us to carry out our research on his greenhouse. We also wish to give special thanks to Víctor Molina, a technician specialized in biological control from Biosur Productos Agrícolas S.L.U., for field assistance.

## Author contributions

Estefanía Rodríguez: Conceptualization, Methodology, Funding acquisition, Investigation, Resources, Writing—original draft, Supervision, Writing—review & editing. Mario Porcel: Formal analysis, Visualization, Writing—review & editing. Lidia Lara: Methodology, Investigation, Writing—review & editing. Tomás Cabello: Formal analysis, Visualization, Writing—review & editing. Manuel Gámez: Formal analysis, Visualization, Writing—review & editing. Leticia Navarro: Investigation, Resources, Supervision. Alberto Domingo: Resources. Francisco Javier Burguillo: Formal analysis. M<sup>a</sup> del Mar Téllez: Conceptualization, Data curation, Methodology, Funding acquisition, Investigation, Resources, Writing—review & editing, Project administration.

## Declarations

### Competing interests

The authors declare no competing interests.

### Additional information

**Correspondence** and requests for materials should be addressed to E.R.

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