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# Tomato-aphid-hoverfly: a tritrophic interaction incompatible for pest management

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**Abstract** Trichome-based tomato resistance offers the potential to reduce pesticide use, but its compatibility with biological control remains poorly understood. We evaluated *Episyrphus balteatus* De Geer (Diptera, Syrphidae), an efficient aphidophagous predator, as a potential biological control agent of *Myzus persicae* Sulzer (Hemiptera, Aphididae) on trichome-bearing tomato cultivars. *Episyrphus balteatus*' foraging and oviposition behavior, as well as larval mobility and aphid accessibility, were compared between two tomato cultivars (*Lycopersicon esculentum* Mill. 'Moneymaker' and 'Roma') and two other crop plants; broad bean (*Vicia faba* L.) and potato (*Solanum tuberosum* L.). Hoverfly adults landed and laid more eggs on broad beans than on three species of Solanaceae. Hoverfly larval movement was drastically reduced on tomato, and a high proportion of hoverfly larvae fell from the plant before reaching aphid prey. After quantifying trichome abundance on each of these four plants, we suggest that proprieties of the plant surface, specifically trichomes, are a key factor contributing to reduced efficacy of *E. balteatus* as a biological agent for aphid control on tomatoes.

**Keywords** *Episyrphus balteatus* ·
*Lycopersicon esculentum* · *Myzus persicae* ·
Trichome-based resistance

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## Introduction

Aphids are major agricultural and horticultural pests throughout the world. While they can result in direct damage to crops through feeding on phloem tissue, they can also contribute to severe indirect damage by acting as primary vectors of many plant viruses. Aphids reproduce rapidly and have been shown to adapt quickly to host-plant phenology and ecology, as well as plant physiology and biochemistry (e.g. Pettersson et al. 2007).

While chemical insecticides can provide adequate control of aphid populations, increased resistance among aphid populations to chemical products highlights the need for alternative control methods, including the use of natural enemies (Cook et al. 2007). In order to increase the effectiveness of such alternative control techniques we need a better understanding of the ecology and behavior within these tri-trophic interactions.

Aphid communities are subject to predation by a broad range of specialist and generalist arthropod predators and parasitoids. Aphid natural enemies such as hoverflies (Gilbert 1986, 2005), coccinellid beetles (Hodek and Honek 1996), lacewings (Principi and Canard 1984), cecidomyiid midges (Nijveldt 1988), spiders (Sunderland et al. 1986) and parasitoids (Stáry 1970), are major components of the natural enemy guild associated with aphid

colonies. Hoverflies are efficient aphidophagous predators (Alhmedi et al. 2008). Our study organism, *Episyrphus balteatus* De Geer (Diptera, Syrphidae), is an economically important syrphid and accepts a broad range of aphid species in the field (e.g. Völkl et al. 2007). Whereas adult hoverflies feed on nectar, pollen, plant saps, and aphids' honeydew, the larvae of this species are voracious predators of aphids and are important biological control agents (e.g. Ankersmit et al. 1986; Chambers and Adams 1986). The complete ventral body side of apodal larvae adheres closely to plant surfaces by greasy smeared saliva. Larvae move by means of body contractions (e.g. Bathia 1939; Brauns 1953; Roberts 1971; Gries 1986; Rotheray 1987). Adults' tarsi are equipped with paired curved claws interlocking with rough surfaces; and additionally, they bear two pulvilli covered with adhesive setae adhering to smooth surfaces (Gorb et al. 2001). Attachment and locomotion are influenced by plant surface qualities and probably important features for prey searching efficiency (Rotheray 1987).

Most predators have been shown to have specific host plant preferences (e.g. Hodek 1993; Schoonhoven et al. 1998; Almohamad et al. 2007, 2008a), and these preferences need to be considered when exploiting them as biological control agents. These preferences are especially important for syrphids because syrphid larvae have limited dispersal abilities (Chandler 1969). Therefore oviposition site discrimination has a strong impact on offspring performance (Scholz and Poehling 2000). The oviposition preference of female syrphids has recently been correlated with offspring performance on preferred host plants (Almohamad et al. 2007). The behavioural impact of various plant and prey secondary metabolites, including volatile and non-volatile chemicals, in the localization and selection of an oviposition site in *E. balteatus* has largely been demonstrated (Chandler 1968; Kan 1988; Sadeghi and Gilbert 2000a, b; Harmel et al. 2007; Almohamad et al. 2008b; Verheggen et al. 2008). Among these chemicals, the main component of the aphid alarm pheromone, the sesquiterpene (E)-$\beta$-farnesene (Francis et al. 2005a), acts as an attractant and an oviposition stimulant for various aphid predators including the ladybeetle *Harmonia axyridis* Pallas and the hoverfly *E. balteatus* (Almohamad et al. 2007, 2008b; Verheggen et al. 2007, 2008, 2009).

While previously studying induced volatile emissions of aphid-infested tomato plants, and the subsequent effect on *E. balteatus* attraction, we observed their apparent failure in aphid control on tomato plants. We therefore estimated in the present study the ability of hoverfly females to orient toward and forage on glandular hairy tomato plants infested by *M. persicae*. We evaluated *E. balteatus* as a possible biological agent against aphids on tomato compared to

potato and broad bean plants. Surfaces of *Lycopersicon* sp. and *Solanum* sp. have been reported to be covered with glandular trichomes (e.g. Luckwill 1943; Gibson 1971), whereas the surface of *V. faba* appears to be glabrous (Hessayon 2003). We observed (1) the host plant preference of female hoverflies considering searching, selection and oviposition behavior as well as (2) the larval locomotion on different plant surfaces.

Trichome-mediated plant defenses are implicated in both the second and the third trophic level (see the review of Kennedy 2003). First, trichomes can provide major resistance against a number of herbivorous arthropods like aphids (Farrar and Kennedy 1991; Simmons et al. 2003), but can also interact directly or indirectly with their natural enemies (Kennedy 2003). The resulting effects might be positive (increased proliferation, decreased cannibalism) (e.g. Seagraves and Yeargan 2006) or negative (impeded searching behavior, lower prey accessibility) (e.g. Obrycki and Tauber 1984; Oku et al. 2006; Economou et al. 2006). Particularly, the presence and density of trichomes have been previously considered to affect insects (e.g. Levin 1973). Both adults and larvae of hoverflies have been reported to be more abundant and better suited to exploiting aphids on smooth, flat surfaces (e.g. Rotheray 1987; Wnuk and Gospodarek 1999; Sadeghi and Gilbert 2000a, b). During centrifugal force experiments, adult *E. balteatus* generated attachment forces on smooth PVC surfaces enabling them to withstand acting centrifugal forces up to the twentyfold of their body weight (20 mg) (Gorb et al. 2001). On hairy leaves of cucumber, bean, and tomato, the mobility of syrphid larvae has been observed to be considerably decreased (Albert et al. 2007). To test the hypothesis that trichome density plays an important role for the predatory success of syrphids on plants, we counted trichomes per unit area of stems, and discussed these data related to obtained observational results.

## Materials and methods

### Plants and insects

Two tomato cultivars *Lycopersicon esculentum* Mill. 'Moneymaker' and 'Roma' (Solanaceae), whose aphid infestations were previously observed to be hardly controlled while using predatory hoverflies (Verheggen, unpublished data), were selected to test larval locomotion and success in reaching aphid colonies. Two additional host plants of *Myzus persicae* Sulzer (Homoptera, Aphididae), namely broad bean *Vicia faba* L. 'Grosse ordinaire' (Fabaceae) and potato *Solanum tuberosum* L. 'Bintje' (Solanaceae), were selected for comparison with

the above mentioned tomato cultivars. *Vicia faba* and *S. tuberosum* were chosen because they were shown in previous work to be easily exploited as host plants by *E. balteatus* (Almohamad et al. 2007; Harmel et al. 2007), and they have different surface proprieties compared to tomato cultivars.

Broad beans were grown in $30 \times 20 \times 5$ cm plastic trays filled with a mix of perlite and vermiculite (1:1). Potato and tomato plants were cultivated in $8 \times 8 \times 10$ cm plastic pots filled with a mix of compost, perlite, and vermiculite (1:1:1). All plants were grown in controlled environment growth rooms (16:8 h light:dark; $20 \pm 2°C$; RH: $70 \pm 5\%$). The peach aphids were reared on the four previously mentioned plants in separate controlled environment growth rooms set at the same conditions as described above. Adult specimens of *E. balteatus* were reared in a separate room, in $75 \times 60 \times 90$ cm cages and were fed with bee pollen, sugar and water. Broad beans infested with *M. persicae* were introduced into the cages for 3 h every 2 days to allow oviposition by hoverfly adults. Hatched hoverfly larvae were mass-reared in aerated plastic boxes ($110 \times 140 \times 40$ mm) and were fed daily ad libitum with *M. persicae* as a standard diet. All the hoverfly adults tested in the following experiments were 2–4 weeks old, which corresponds to sexual maturity and high fecundity (Sadeghi and Gilbert 2000c), and had not previously been exposed to aphid-infested plants.

Host plant preference of female hoverflies

In no-choice experiments, hoverfly females were individually placed in screened cages ($30 \times 30 \times 60$ cm) with one of the four tested plant species infested with 100 adult *M. persicae* 24 h prior to observations. Plants, roughly 20 cm tall, having four fully expanded leaves were presented in a plastic pot filled with the same soil composition as presented above. The soil was covered with aluminum foil to avoid any volatile chemicals released by the compost to affect the hoverfly behavior. The hoverfly foraging behavior was visually observed and recorded for 10 min using the Observer® software (Noldus Information Technology, version 5.0, Wageningen, The Netherlands). Descriptions of the five observed behavioral subdivisions (Immobility, Flying, Searching, Acceptance, Oviposition) are presented in Table 1.

In another series of similar no-choice experiments, single *E. balteatus* females were allowed to lay eggs for 3 h and the number of eggs laid on each aphid infested plant was counted. The experiments were conducted at a controlled temperature of $20 \pm 2°C$, and relative humidity of $70 \pm 5\%$. *E. balteatus* females were 21–28 days old. One female per each plant was tested. There were a total of 20 replicates for each of the two aforementioned experiments.

**Table 1** Description of the behavioral events recorded for female hoverfly *Episyrphus balteatus* in no-choice experiments, exposed separately to individuals of four different aphid infested host plants for 10 min

| Observed behavior | Description |
|---|---|
| Immobility | Immobile on the cage |
| Flying | Flying far from the plant (>5 cm) |
| Searching | Flying near the plant (<5 cm) |
| | Touching sporadically the plant |
| Acceptance | Landing and walking on the plant |
| | Extending its proboscis and identifying the simulatory substrate to accept the host |
| Oviposition | Laying eggs on the plant surface |

Observation of larval locomotion

In above mentioned net cages, 20 cm tall plants were infested by placing 20 adult *M. persicae* on the adaxial surface of two fully expanded leaves. All other lower leaves were manually removed from the plant. Aphids were allowed to feed 4 h before starting the experiment. After this initial aphid settlement period a third instar larva of *E. balteatus*, starved 5 h prior to the experiment, was placed in the middle of the plant on the stem, oriented to face the top of the plant. Twenty hoverfly larvae were observed separately on 20 individual plants per each of the four above mentioned test plants. Three types of reactions were observed ocularly and recorded: (1) When a larva moved and reached the top of the plant within 15 min of placement on the plant, (2) when a larva fell from the plant within 15 min of placement on the plant, and (3) when a larva remained stationary or did not reach the top of the plant within the 15 min of observation. Each plant and insect was tested once.

The average larval locomotion speed was calculated by taking into account the larvae that reached the top of the plant within the 15 min of observation. Larval locomotion speed (mm s$^{-1}$) was calculated as the distance traveled divided by the time needed to reach the top of the plant.

Evaluation of trichome density

To correlate the impact of trichome density with the host plant preference of female, and with the locomotion speed of larval hoverflies, we quantified the trichome density by counting the number of trichomes per square centimeter of stem surface under the binocular microscope Olympus® SZ40 (Olympus Corporation, Tokyo, Japan). Digital images were taken using a Canon® 450D equipped with a 100 mm f2.8 Canon® macro lens (Canon Corporation, Tokyo, Japan). A 1 cm long piece of the stem was cut with

a razor blade from the middle of a 20 cm tall plant with four fully expanded leaves. Ten plants of each of the four tested cultivars were cut this way. According to Luckwill (1943) and Simmons and Gurr (2005), there are up to five types of glandular and non-glandular trichomes found on a *L. esculentum* (named types I, III, V, VI, VII). Glandular trichomes have 'heads' that release, on contact with pests, sticky and/or toxic exudates that entrap, irritate and potentially kill the pest. Non-glandular trichomes have no 'heads' releasing sticky and/or toxic exudates and may affect pests by mechanical means (e.g. constituting a barrier to movement or access to nutritious source(s)) (Simmons and Gurr 2005). We considered only trichomes of types I and III reaching a length of 1.0–2.5 mm for the determination of trichome density. In *S. tuberosum*, all trichomes of more than 1.0 mm were counted. Indeed, according to our observations, no contact occurred between the body of the tested third instar hoverfly larvae (being usually larger than 7 mm) and the smallest trichomes of types V, VI and VII, ranging from 0.05 to 0.5 mm (Fig. 1).

Statistical analyses

One-way ANOVA followed by *Tukey's* post-hoc test (pairwise comparisons) were used to evaluate data obtained in the host plant preference experiment (Minitab® release 14.2 software, Minitab Inc., State College, PA, USA). A general linear model followed by *Tukey's* test (pairwise comparisons) was used to compare the average larval locomotion speed observed on the four tested host plants.

**Results**

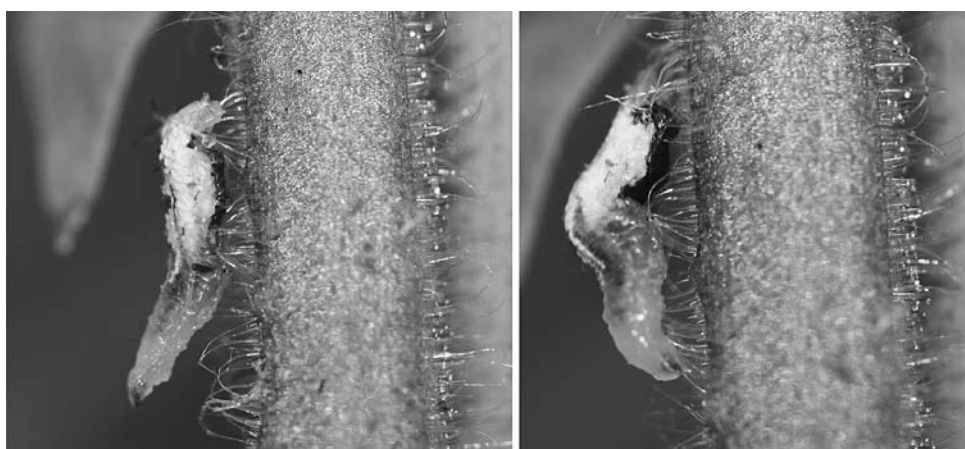Host plant preference of female hoverflies

In no-choice experiments, the relative durations of the five observed behavioral subdivisions (Immobility, Flying, Searching, Acceptance, Oviposition) were recorded. Relative durations of the 'Immobility' and 'Searching' behavior were similar for the four plants tested (ANOVA, Tukey post-hoc test, $P > 0.05$). However, hoverfly females spent more of their time (recorded as acceptance) on *V. faba* than on *S. tuberosum* and *L. esculentum* 'Moneymaker' (ANOVA, $F_{3,76} = 4.66$, $P = 0.005$, Tukey post-hoc test) (Fig. 2). In addition, the relative duration spent ovipositing on broad bean plants was greater than on the three species of Solanaceae (ANOVA, $F_{3,76} = 6.50$, $P = 0.001$, Tukey post-hoc test). These observations are in accordance with the number of eggs laid on each of the four tested plants. An average ($\pm$ SE) of $28.65 \pm 5.48$ eggs were laid on *V. faba*. Significantly fewer eggs were laid on *S. tuberosum* and *L. esculentum* 'Roma' and 'Moneymaker', with $8.95 \pm 2.69$, $11.80 \pm 2.60$ and $10.75 \pm 3.69$ eggs respectively (mean $\pm$ SE) (ANOVA, $F_{3,76} = 5.81$, $P = 0.001$, Tukey post-hoc test).

Larval locomotion

To evaluate the ability of *E. balteatus* larvae to reach their aphid prey, their locomotion was observed, and the locomotion speed was recorded on each of the four plants was recorded (Fig. 3). Only the larvae that reached the top of the plant within the 15 min of observation were taken into account in the calculation of the average larval locomotion speed: 11, 10, 4, and 5 larvae for *V. faba*, *S. tuberosum*, *L. esculentum* 'Roma' and 'Moneymaker' respectively. The average ($\pm$ SE) locomotion speed of hoverfly larvae on *V. faba* ($2.7 \pm 0.37$ mm s$^{-1}$) was significantly higher than on both tomato cultivars, 'Roma' ($0.8 \pm 0.33$ mm s$^{-1}$) and 'Moneymaker' ($0.7 \pm 0.23$ mm s$^{-1}$) (ANOVA, $F_{3,26} = 4.23$, $P = 0.015$, Tukey post-hoc test). The average ($\pm$ SE) larval speed on *S. tuberosum* ($1.44 \pm 0.47$ mm s$^{-1}$) did not differ significantly from the speed values on the three other aphid host plants tested. In addition, the number of larvae that fell from the plant was counted. No larvae fell from



**Fig. 1** Digital images of third instar hoverfly larvae moving on the glandular hairy stem surface of *Lycopersicon esculentum* 'Moneymaker', showing two different positions of the locomotion process. Larvae adhere to the tips of long trichomes, without direct contact between the insect body and the solid stem surface

**Fig. 2** Host plant preference of *Episyrphus balteatus* females in no-choice experiments with four different aphid-infested host plants indicated by behavioural characteristics (% of the 10 min total observation time + SE). Different letters indicate significant differences between plant species and cultivars for a single behaviour characteristic (*n* = 20; for detailed statistical values see results section)
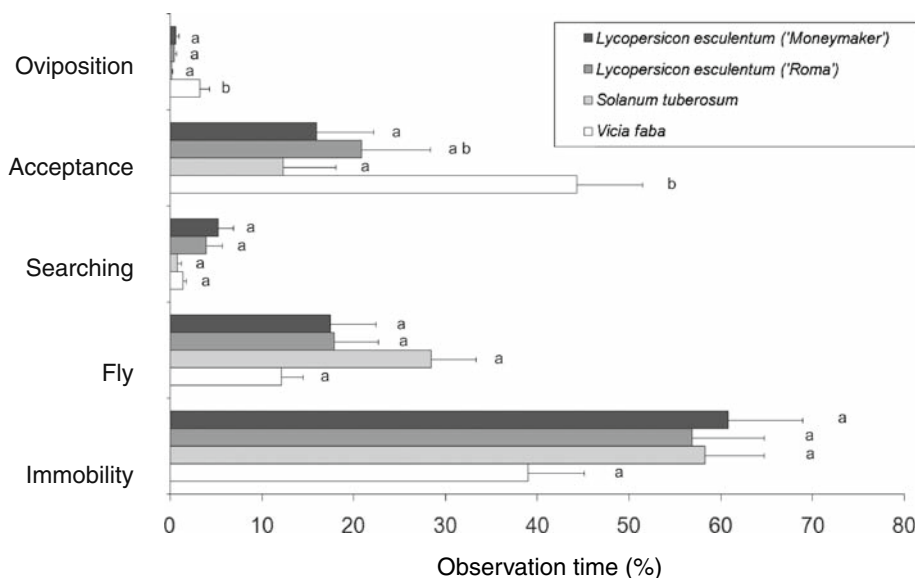
V. faba and one larva fell from *S. tuberosum*. On *L. esculentum*, 50% ('Roma') and 25% ('Moneymaker') of the larvae fell while walking on the glandular hairy plant surface.

Trichome density

While no trichomes were found on the plant surface of *V. faba*, an average (± SE) of 16.84 ± 2.08 trichomes were present per $cm^2$ of *S. tuberosum* stem. *L. esculentum* 'Moneymaker' and 'Roma' had 68.32 ± 5.31 and 72.32 ± 5.46 trichomes (mean ± SE, types I and III pooled together) per $cm^2$ of stem, respectively (Fig. 4). Trichome densities were significantly different between *S. tuberosum* and both *L. esculentum* cultivars, but not between the two tomato cultivars (ANOVA, $F_{2,27} = 46.01$, $P < 0.001$, Tukey post-hoc test).

**Discussion**

Insect–plant interactions involving the genus Lycopersicon, their herbivores and herbivore natural enemies have been previously studied by several authors, and reviewed by Kennedy (2003). Beside the beneficial impact of their volatile chemicals on infesting pests (Ecole et al. 2001), trichome-based natural resistance of tomato plants offers a potential approach to reduce pesticide use (McKinney 1938). Trichomes are usually implicated in the second trophic level by increasing pest mortality, as demonstrated within numerous host plant models including tomatoes (e.g. Johnson 1956; Musetti and Neal 1997) and potatoes (e.g. Gibson 1971, 1974). For example, the glandular trichomes of the wild potato species, *Solanum berthaultii* Hawkes, deter oviposition and affect other important performance parameters of the potato tuber moth, *Phthorimaea*

**Fig. 3** The larval locomotion speed (mean ± SE) and the number of larvae falling off of the stem depending on the host plant. Different letters indicate significant differences in larval speed between plant species (see figure for number of replicates; for detailed statistical values see Results section)
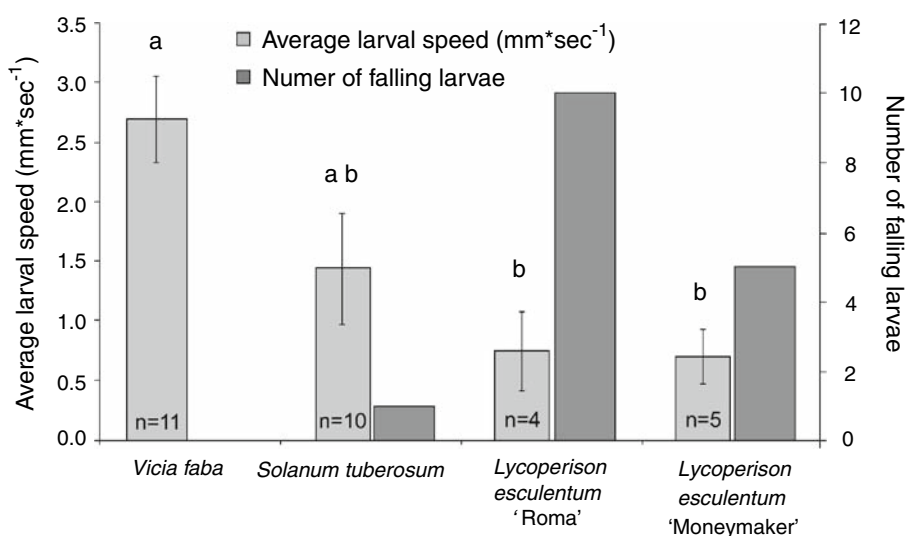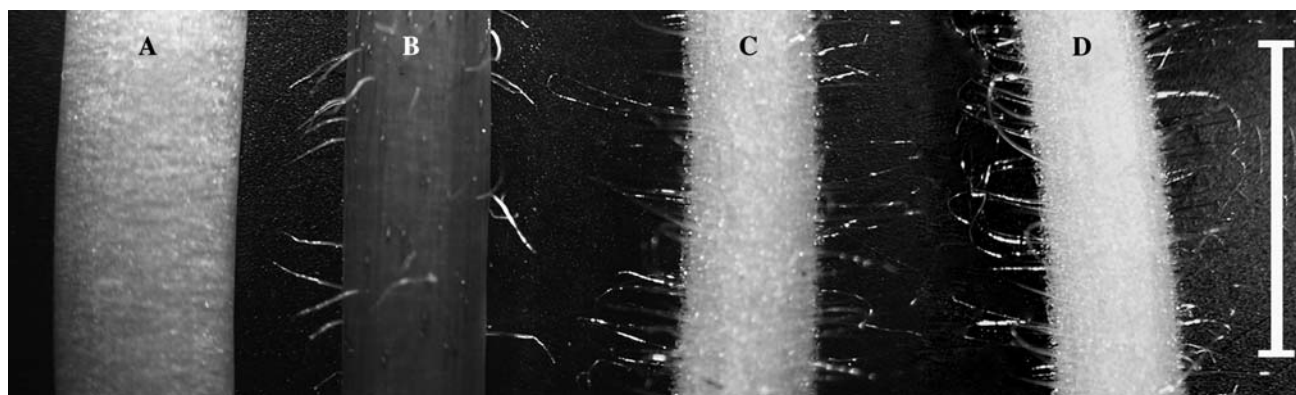
**Fig. 4** Digital images of the middle part of the stem of the three plant species tested, showing distinct pubescence in the representatives of Solanaceae. (A) *Vicia faba*, (B) *Solanum tuberosum*, (C) *Lycopericon esculentum* 'Roma', (D) *Lycopersicon esculentum* 'Moneymaker'. Scale bar = 1 cm

*operculella* Zeller (Lepidoptera, Gelechiidae) (Malakar and Tingey 2000). The feeding behavior of the potato aphid *Macrosiphum euphorbiae* Th. (Hemiptera, Aphididae) was deterred by glucose esters present in glandular trichome exudates of the wild tomato, *Lycopersicon pennellii* Corr. (D'Arcy) (Goffreda et al. 1989). However, the compatibility of trichome abundance with biological control agents remains sometimes unclear, although it is well known that they are also implicated in the third trophic level. Indeed, trichomes affect natural enemies either by direct contact or indirectly by positively affecting the phytophagous prey insect (e.g. Simmons et al. 2003; Oku et al. 2006). However, interactions between plant surfaces and hoverfly aphidophagous predators have previously received little attention.

When looking for suitable oviposition sites, hoverfly females are able to discriminate between aphid species as well as between host plants on the basis of the released odorant cues (Bargen et al. 1998; Almohamad et al. 2007; Verheggen et al. 2008). When landed on a plant, hoverflies use tactile foraging, through extension of their proboscis, before laying their eggs. Broad beans, *V. faba*, have been largely used in the study of the oviposition behavior of hoverflies, demonstrating its suitability for this aphidophagous predator within pest management strategies (e.g. Vanhaelen et al. 2001; Francis et al. 2005b; Verheggen et al. 2008). Potatoes have also been presented as suitable host plants for hoverfly female oviposition (e.g. Verma et al. 2005; Harmel et al. 2007; Almohamad et al. 2007). In our behavioral experiments, the negative effect of trichomes on the accessibility of hoverfly adults was visually observed. In no choice experiments, we showed that *E. balteatus* females were landing and laying eggs more frequently on *V. faba* rather than on the three Solanaceae studied, which is likely to lead to a more efficient foraging of aphid preys. Our findings correspond to observations of previous authors who reported higher abundance of hoverflies on *V. faba* and other plants having non-hairy surface compared to these

ones with trichome coverage (e.g. Wnuk and Gospodarek 1999). Although hoverfly females were flying close to tomato plants (see "searching behavior" in Fig. 1), they had clear difficulties in landing, presumably due to the presence of long trichomes of types I and III.

Increased trichome density can reduce aphid accessibility, but can also affect negatively predator efficacy through increased predator cannibalism, predator mortality due to entrapment by trichomes or falling off the plant. Accordingly, the ability of the lacewings *Mallada signata* Schneider (Neuroptera, Chrysopidae) to be used as biological control agents against aphids on pubescent tomato plants has been questioned in previous work, showing that densely arranged trichomes cause a decreasing number of predated aphids and increased cannibalism and entrapment-related predator mortality (Simmons and Gurr 2004). The presence of trichomes is also known to reduce the residence time and foraging efficiency of larval lacewings *Chrysoperla* spp. (Neuroptera, Chrysopidae), which are further representatives of components of the aphid predatory guild (Gassman and Hare 2005). Two other aphid predators, *Macrolophus pygmaeus* Rambur (Heteroptera, Miridae) and *Orius niger* Wolff (Heteroptera, Anthocoridae), have been also reported to be negatively influenced by the density of glandular trichomes on the surface of tomato plants (Economou et al. 2006). The bugs spent most of their time grooming instead of searching for prey because they were in touch with exudates that accumulated on their tarsi. *Orius insidious* Say, a mite predator, has shown also greater foraging ability on smooth plant surfaces than on tomato plant (Coll et al. 1997).

Trichome density on the stem surface of tomatoes has also an influence on the foraging speed of hoverfly larvae. Many larvae fell while trying to reach the top aphid-infested leaves of tomato plants, supporting previous observations of a considerably decreased mobility of syrphid larvae on hairy leaves cucumber, bean, and tomato (Albert et al.

2007). While no information on larval mobility has been reported for *Solanum* sp., the hoverfly larvae have been shown to have strong predatory potential on these plant species (Verma et al. 2005). Although the locomotion of hoverfly larvae was observed to be reduced on potato (compared to broad beans) obviously because of its pubescence, the locomotion speed did not statistically differ, and only one of the 20 hoverfly larvae tested on *S. tuberosum* fell from the plant. Entomophagous insects (Coccinellidae, Chrysopidae, Thripidae, Anthocoridae, parasitoids) have been widely reported to be hampered by pubescent plant surfaces in numerous publications (e.g. Putman 1955; Rabb and Bradley 1968; Shah 1982). However, these results contrast with those obtained in studies of specialized predators like fire ants of the species *Solenopsis invicta* Buren (Hymenoptera: Formicidae) (Styrsky et al. 2006) and the coccinellid *Coleomegilla maculata* DeGeer (Coleoptera, Coccinellidae) (Seagraves and Yeargan 2006). The latter prefers to oviposit on plants having glandular trichomes that would provide the eggs a refuge from cannibalism and other predation. The omnivorous mirid bug *Dicyphus errans* Wolff (Heteroptera, Miridae) preys on a variety of phytophagous arthropods living on pubescent plants that provide the bug stronger attachment and therefore more reliable locomotion as well as more successful oviposition and predation (Voigt et al. 2007). The contrary observations realized in our study with *E. balteatus* may be caused by different morphological features. Unlike above mentioned predators, syrphid larvae do not bear long articulating legs.

Although apodal syrphid larvae are known to form a close contact with glabrous plant surface (e.g. Brauns 1953; Wyss 2004), we observed larvae of *E. balteatus* somehow moving along tips of long trichomes on the surface of tomato stems. However, compared to the smooth surface f broad beans, larval attachment and mobility were strongly limited by the abundance of trichomes in Solanaceae. But furthermore, the type, arrangement, dispersion, anatomy properties, and geometrical variables of trichomes may influence insect attachment to and locomotion on plant surfaces (e.g. Voigt et al. 2007). In particular, sticky exudates of glandular trichomes may contaminate insects (Kennedy 2003; Voigt et al. 2007), which may be also possible in *E. balteatus* contacting glandular hairy plant surfaces. The effects of trichomes may be more apparent on apodal syrphid larvae than on leg-bearing predators like, e.g. representatives of Heteroptera able to interlock with trichomes using claws, and having distinct distance from the plant surface due to their long legs. However, in both females and apodal larvae of the predatory midge *Aphidoletes aphidimyza* Rondani (Diptera, Cecidomyiidae), which larvae have similar locomotion and foraging strategies like those of syrphids, the higher density of trichomes,

the more eggs were laid and the more egg survival was observed (Lucas and Brodeur 1999). But compared to syrphid larvae, predatory midges have a distinctly smaller body size, possibly enabling them to move easily on the smooth patches of the plant surface between trichomes. In contrast, larger syrphid larvae, contacting only trichome tips, may be affected by the larger trichomes that act as a hurdle for larval locomotion.

Our results show that the plant surfaces covered densely with trichomes are not suitable for both hoverfly female and larva foraging, although no statistical regressions have been carried out. We showed that the attachment and locomotion of the predatory larvae of *E. balteatus* is compromised on solanaceous plants densely covered with glandual trichomes, particularly on *L. esculentum* cultivars. Therewith, larval mobility and subsequent aphid accessibility are decreased. However, trichome density does not seem to be the single hampering plant surface feature for syrphid access, which should be analysed in further studies.

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