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RESEARCH ARTICLE

Effect of Host Plant of Aphididae, Plant Structure and Aphid Alarm Pheromone on Oviposition by Ladybirds

Omkar
Department of Zoology, University of Lucknow, Lucknow-226007, India

ABSTRACT

In the class Insecta, the chemistry of the oviposition site is crucial element for offspring survival. Thereby, females tend to choose specific sites on the specific host plants that offer better nutrition and support for larval development. Alarm pheromones, released in response to predation, serve as chemical cues influencing predator behaviour. The present study investigates the effects of aphid-host plant associations, plant architecture, and aphid alarm pheromone on oviposition behaviour in four ladybird species, *viz*. *Coccinella septempunctata, Coccinella transversalis, Menochilus sexmaculatus* and *Propylea dissecta*. The effect of these associations were found to be species-specific. Females laid the highest number of eggs on *Aphis gossypii- Lagenaria vulgaris* and *Aphis craccivora-Dolichos lablab* aphid-plant complexes. Lowest oviposition was reported on *A. gossypii-Solanum melongena* and *A. craccivora-Vigna unguiculata* complexes. Among plant structures, maximum oviposition was observed on bean pods and young leaves, whereas old leaves were the least preferred oviposition site. The presence of alarm pheromone from *Acyrthosiphon pisum* significantly enhanced oviposition in all four ladybird species. These findings highlight the importance of tri-trophic interactions in shaping oviposition decisions and suggest potential strategies for enhancing biological control through habitat manipulation.

KEY WORDS: Coleoptera; *Coccinia grandis*; *Dolichos lablab*; *Lagenaria vulgaris*; *Solanum melongena*; *Vigna unguiculata*.

INTRODUCTION

Oviposition site selection in insects is a critical determinant of offspring survival and fitness, particularly among biocontrol agents such as ladybird beetles (Coleoptera: Coccinellidae). This process of oviposition site selection is influenced by a complex interplay of biotic and abiotic factors, including host plant chemistry, plant architecture, and semiochemicals emitted by prey. In Coleopterans, oviposition is often stimulated by chemical cues released by aphids (Hemiptera: Aphididae) on host plants, which serve as indicators of prey availability and habitat suitability (Seagraves, 2009; Lundgren, 2011).

Female ladybirds optimize oviposition sites by balancing multiple ecological parameters: (a) microclimatic conditions conducive to embryonic development (Pasteels *et al*., 1986), (b) nutritional quality and abundance of prey for larvae (Mishra *et al*., 2013; Hodek *et al*., 2012), (c) protection from predators and competitors (Dixon, 2000; Mishra *et al*., 2012), and (d) spatial distribution and structural complexity of host plants (Omkar *et al*., 2011; Giles *et al*., 2002a,b).

While ladybirds are generally polyphagous, their reproductive success varies significantly with aphid species and the host plants on which these aphids are reared (Michaud, 2000; Kalushkov & Hodek, 2004; Omkar & Mishra, 2005; Omkar *et al*., 2009). Host plant traits such as leaf texture, sap content, and secondary metabolites can influence aphid suitability and, consequently, predator fecundity and larval development (Wu *et al*., 2010; Larsson *et al*., 2000; Awmack & Leather, 2002).

Plant architecture adds another layer of complexity to oviposition behaviour. Features such as leaf size, branching angles, and surface morphology affect predator mobility, prey accessibility, and microhabitat

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*Email: omkar.lkouniv@gmail.com

availability (Andow & Prokrym, 1990; Robert *et al*., 2002). For instance, while most coccinellids lay eggs on leaf surfaces (Klausnitzer & Klausnitzer, 1986), species like *Megalocaria dilatata* prefer spines or concealed structures, suggesting adaptive strategies to minimize egg predation and environmental stress (Liu, 1933). Similar oviposition preferences have been observed in aquatic insects such as *Lestes macrostigma*, which lay eggs in submerged shoots to enhance offspring survival (Lambret *et al*., 2018).

Chemical cues, particularly aphid alarm pheromones like (E)-β-farnesene, play a pivotal role in prey detection and oviposition site selection (Nakamuta, 1991; Hatano *et al*., 2008). These volatiles not only signal the presence of prey but also enhance predator foraging efficiency and reproductive output. Chemical cues are involved in the host location and oviposition. They also provide the signals to foraging predatory insects about the location of their prey. The behavioural events of the insects are associated with their sensory (*e.g.* olfaction, vision, taste) cues to feed or oviposit on a particular plant surface (Derridj *et al*., 1996; James, 2005; Sarmento *et al*., 2007; Seagraves, 2009). In previous studies including olfactometeric measurements revealed that young larvae of Coccinellids were significantly attracted to the odour of crushed aphids or directly feeding on aphids, but not to that of aphids or larvae, larvae plus aphids or larvae feeding on an artificial diet (Derridj *et al*., 1996). Lacewing, *Chrysopa sinica,* aphid parasitoid, *Aphidius sp.* and *Coccinella septempunctata* all responded to the volatiles released from the tea aphids, *Toxoptera aurantii* (Han & Chen, 2002). Studies on Coccinellidae have shown that *C. septempuntata* were observed more on the plants with heavy infestation of soybean aphids, *Aphis glycines* (Zhu & Park, 2005).

The chemical cues not only play the role between the communication of Aphididae and Coccinellidae but also between the other prey-predators too. Volatile and non-volatile compounds are synthesized by the plants when they are damaged by herbivores. Predators, parasitoids and predatory mites locate their host by using volatile semiochemicals emitted from their hosts or from other food plants infested by their host (Boom *et al*., 2004; Boer & Dicke, 2004). It was reported that volatile chemicals emitted from the honey dew by *Aphis gossypii* Glover on eggplant, *Solanum melongena* (Solanaceae) attracted adult female *Aphidoletes aphidimyza* but there was no known oviposition stimulant (Higashida *et al*., 2022). The pheromone induces perceiving individuals to stop feeding, disperse locally, and often drop from the host plant (Braendle & Weisser, 2001). (E)-β-farnesene also acts as a kairomone, *i.e.* used by predators and parasitoids to locate their prey (Verheggen *et al*., 2007; Verheggen *et al*., 2008). Probably predators easily identify the alarm pheromones which are helpful for searching the prey and the oviposition site.

The ability of natural enemies to reproduce within cropland and effectively suppress pests depends on the presence of plants on which they can oviposit within the agroecosystems. In the present study we have used selected plant structures of *Vicia faba* such as old leaves, young leaves, tendrils and bean fruits. These traits might affect the decision of the oviposition site selection by Coccinellids due to the tendency of aphids to feed on moist, soft and concealed structure of plants such as within the rolls of furled, immature leaves or within the junctions of the blade and sheath of mature leaves (Burd & Burton, 1992; Reed & Kindler 1992). Studies have shown that ladybirds and other aphidophagous insects respond strongly to volatiles emitted from aphid-infested plants or crushed aphids (Han & Chen, 2002; Zhu & Park, 2005; Verheggen *et al*., 2007).

In agroecosystems, the ability of natural enemies to reproduce and suppress pest populations depends on the availability of suitable oviposition substrates. Aphids tend to colonize soft, moist, and concealed plant structures such as young leaves and tendrils (Burd & Burton, 1992; Reed *et al*., 1992), which may influence ladybird oviposition preferences. Understanding these tri-trophic interactions is essential for enhancing biological control strategies.

This study investigates the effects of (i) aphid-host plant complexes, (ii) plant structural traits, and (iii) aphid alarm pheromones on oviposition behaviour in four common ladybird species: *Coccinella septempunctata, Coccinella transversalis, Menochilus sexmaculatus*, and *Propylea dissecta*. By examining species-specific responses to these ecological variables, we aim to elucidate the mechanisms underlying oviposition site selection and contribute to the optimization of predator-based pest management.

MATERIALS AND METHODS

Stock maintenance

Fifty adults each of *Coccinella septempunctata, Coccinella transversalis, Menochilus sexmaculatus*, and *Propylea dissecta* (henceforth C7, Ct, Ms and Pd respectively) were collected from agricultural fields surrounding Lucknow, India (26º 50'N, 80º 54'E). They were paired for mating in transparent plastic Petri dishes (9.0 × 2.0 cm) containing *Acyrthosiphon pisum* on the leaves of host plant *Vicia faba* L. (Fabaceae) taken from glasshouse cultures (maintained at 21±1ºC; 65±5% R.H.) under laboratory conditions (27±1ºC; 65 ± 5% R.H.; 14L: 10D). Males were removed after mating. Food was replaced, the eggs laid were collected every 24h and incubated under the above abiotic conditions until hatching. The larvae were reared until adult emergence in plastic beakers (14.5 × 10.5 cm; 5 larvae per beaker). The required stages were taken from the stock for experiment.

Experimental design

The following three treatments were designed to investigate the effect on oviposition by the ladybirds.

(A) Effect of aphid-host plant complexes : To evaluate aphid-host plant associations, fresh tender leaves of *Solanum melongena* L. were placed in a Petri dish (14.5 × 1.5 cm). The second and third instar *Aphis gossypii* Glover, reared on the same plant, were carefully transferred into the petri dish (size as above). The aphids were allowed to settle on the leaf surface and initiate feeding, ensuring host plant recognition and physiological engagement prior to further experimental manipulation. This setup provided a controlled environment to observe aphid behaviour and subsequent interactions with predatory coccinellids. Thereafter, a single10-day-old once-mated female of C7, Ct, Ms or Pd was introduced in the Petri dish. After 24h, the number of eggs laid by the Coccinellids, was recorded. This procedure was repeated using *A. gossypii* reared on different host plants *viz., Lagenaria vulgaris* Seringe (Cucurbitaceae) and *Coccinia grandis* L. (Cucurbitaceae). To assess whether aphid species and host plant identity influence oviposition behaviour of ladybirds, similar procedure was followed for another aphid species, *Aphis craccivora* Koch reared on two host plants, *Dolichos lablab* L. (Fabaceae) and *Vigna unguiculata* L. (Fabaceae) (n = 10 per treatment) .

(B) Effect of plant structure : Ten-day-old focal females (C7, Ms, Ct and Pd) were placed individually in plastic Petri dishes (14.5 × 1.5 cm) containing different plant parts (*i.e.,* old leaves, young leaves, tendrils and bean pods) of *D. lablab* infested with *A. craccivora* (*ad libitum*). Leaves were distinguished morphologically on the basis of their texture. Young leaves were moist and soft whereas old leaves were dry and rough. Young and soft tendrils and bean pods were taken for the study. After 24h the number of eggs laid was recorded. This protocol was also repeated on other host plant, *V. unguiculata* (n = 10 per treatment).

(C) Effect of aphid alarm pheromone : *Acyrthosiphon pisum* (50 mg weighed on Sartorius CP225-D; 0.01mg precision) were crushed for 30 seconds with a glass rod in a 50 ml vial. This freshly prepared paste of crushed aphids was then quickly smeared in plastic Petri dish (14.5 × 1.5 cm) with the help of fine camel hair brush. Thereafter *ad libitum A. pisum* (live) was provided in the same Petri dish. These two combinations were provided as a food for 10-day-old focal females of C7, Ct, Ms and Pd. After 24h the number of eggs laid was recorded. For the control treatment, females (n = 10 per treatment) were placed in Petri dishes without crushed aphids paste but equal amount of live aphids and the above mentioned observations were recorded.

Statistical analysis

Data were checked for normality and heterogeneity of variance following Kolmogorov-Smirnov's and Bartletts' test and found to be normally distributed with homogeneity of variances.

Data obtained in experiment A (effect of aphid-host plant complexes) was subjected to two-way ANOVA for both *A. gossypii* and *A. craccivora* with species (C7, Ct, Ms, Pd) and aphid-host plant complexes [*A. gossypii* (on *S. melongena*, *L. vulgaris* and *C. grandis*) and *A. craccivora* (on *D. lablab* and *V. unguiculata*)] as independent factors and number of eggs laid by focal females as dependent factor followed by Tukey's post hoc comparison of means.

To assess the effects of different plant architecture (Experiment B) on oviposition (dependent factor), two-way ANOVA was conducted for both *D. lablab* and *V. unguiculata* with species (C7, Ct, Ms, Pd) and plant architecture (old leaves, young leaves, tendrils and bean pods) as independent factors followed by Tukey's post hoc comparison of means.

Table 1: Oviposition by ladybird females in presence of varying aphid-host plant complexes

Host plant infested with *A. gossypii*	Species	Oviposition
S. melongena	*C. septempunctata*	17 ± 2.7 b(A)
	C. transversalis	12 ± 2.9 ab(A)
	M. sexmaculatus	23 ± 2.4 c(A)
	P. dissecta	7.8 ± 2.2 a(A)
L. siceraria	*C. septempunctata*	45.3 ± 2.1 d(C)
	C. transversalis	24.8 ± 1.4 b(C)
	M. sexmaculatus	35.9 ± 1.5 c(C)
	P. dissecta	19.7 ± 1.5 a(C)
C. grandis	*C. septempunctata*	39.9 ± 1.8 d(B)
	C. transversalis	20.4 ± 1.7 b(B)
	M. sexmaculatus	31.6 ± 1.3 c(B)
	P. dissecta	15.8 ± 1.2 a(B)

Values are Mean±SE

Small alphabets represent comparison of means between focal females within each plant species, and capital alphabets in parentheses represent comparison of means between different plant species within each focal female.

Values followed by different alphabets show significant differences amongst means of a species.

For the effect of aphid alarm pheromone, data obtained from Experiment C (crushed aphids along with same intact aphids) was also subjected to two-way ANOVA with species (C7, Ct, Ms, Pd) and combination (crushed + live aphids) as independent factors and number of eggs laid by focal females as dependent factor followed by Tukey's post hoc comparison of means. All statistical analyses were performed using MINITAB 16.0.

RESULTS

(A) Effect of aphid-host plant complexes

The results revealed that in the presence of *A. gossypii,* oviposition by focal females varied significantly with the ladybird species (F= 15.56; P=0.001; df=3, 119) and aphid-host plant complexes (F= 15.93; P=0.001; df=2, 119). The interaction between species and aphid-host plant complexes was significant (F= 2.42, P=0.026, df=6, 119). The oviposition was maximum on *A. gossypii-L.vulgaris* complex and minimum on *A. gossypii-S. melongena* complex in all four ladybird species. C7 oviposited maximum on *L. vulgaris* and *C. grandis* followed by Ms, Ct and Pd. *Menochilus sexmaculatus* oviposited maximum on *S. melongena* followed by C7, Ct and Pd. (Table 1).

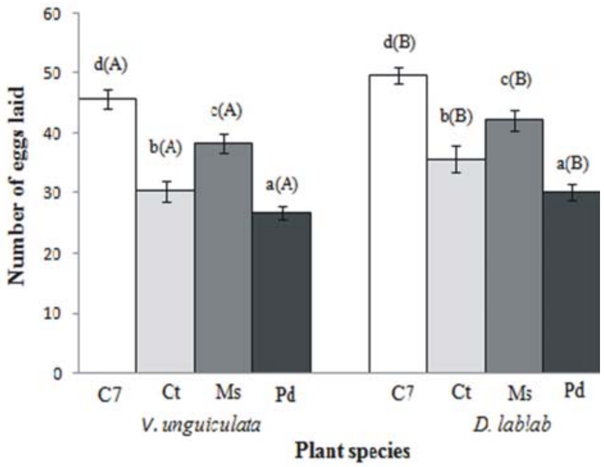

Fig.1. Mean (±SE) numbers of eggs laid in 24 h by 10 day old female ladybirds (n = 10) in 14.5 × 1.5 cm Petri dishes in the presence of *A. craccivora* infested two different host plant species.

Value are Mean ± SE.

For each plant species, small and capital alphabets (placed in parentheses) represent comparison of means between different focal females within and between plant species, respectively. Values followed by different alphabets show significant differences amongst means of a species.

ANOVA revealed significant influence of ladybird species (F=11.63; P=0.001; df=3, 79) and aphid-host plant complexes (F=6.61; P=0.011; df=1, 79) on the numbers of eggs laid by focal females (C7, Ct, Ms and Pd) in the presence of *A. craccivora*. While interaction between species and aphid-host plant complexes (F= 0.05, P=0.983, df=3, 79) was insignificant. All the species laid maximum eggs on *A. craccivora-D. lablab* complex than on *A. craccivora-V. unguiculata* complex. Post hoc analysis revealed that C7 oviposited maximally as compared to Ct, Ms and Pd on both plants (Fig. 1).

(B) Effect of plant architecture

The results of two-way ANOVA revealed that oviposition by Ms females in the presence of different architectures (old leaves, young leaves, tendrils and bean pods) of *D. lablab* plant varied significantly with ladybird species (F= 9.70; P=0.001; df=3, 159) and plant architecture (F= 24.15; P=0.001; df=3, 159). The interaction between species and plant architecture (F= 3.42, P=0.034, df=9, 159) was significant.

ANOVA revealed that ladybird species (F= 211.33; P=0.001; df=3, 159) and plant architecture (F= 37.44;

Table 2: Oviposition by ladybird females in the presence of varying plant architecture of *D. lablab* and *V. unguiculata* infested with *A. craccivora*

Plant architecture	Species	*A.craccivora* on *D. lablab*	*A.craccivora* on *V. unguiculata*
Old leaves	*C. septempunctata*	40 ± 2.1 d(A)	39.1 ± 1.5 d(A)
	C. transversalis	29.7 ± 2.1 b(A)	25.6 ± 1.3 b(A)
	M. sexmaculatus	33.4 ± 1.3 c(A)	30.5 ± 1.2 c(A)
	P. dissecta	20.1 ± 1.2 a(A)	20.2 ± 1.9 a(A)
Young leaves	*C. septempunctata*	45.9 ± 2.2 c(B)	49.7 ± 1.5 d(D)
	C. transversalis	37.1 ± 1.7 b(B)	35.7 ± 1.7 b(D)
	M. sexmaculatus	41.3 ± 1.6 b(C)	41.8 ± 1.6 c(D)
	P. dissecta	29.6 ± 1.5 a(C)	30.9 ± 1.3 a(D)
Tendrils	*C. septempunctata*	44.8 ± 2.7 d(AB)	42.7 ± 1.2 d(B)
	C. transversalis	31.2 ± 1.6 b(AB)	28.9 ± 1.1 b(B)
	M. sexmaculatus	36.8 ± 1.1 c(B)	34.3 ± 1.5 c(B)
	P. dissecta	23.5 ± 1.4 a(B)	24.2 ± 1.2 a(B)
Bean pods	*C. septempunctata*	55 ± 2.8 d(C)	45.8 ± 1.4 d(C)
	C. transversalis	42.6 ± 1.3 b(C)	31.8 ± 1.2 b(C)
	M. sexmaculatus	47.7 ± 2.1 c(D)	38.2 ± 1.4 c(C)
	P. dissecta	33.5 ± 1.4 a(D)	27.6 ± 1.5 a(C)

Values are Mean ± SE.

For each plant species, small alphabets represent comparison of means between focal females within each plant architecture, and capital alphabets in parentheses represent comparison of means between different plant architecture within each focal female.

Values followed by different alphabets show significant differences amongst means of a species.

P=0.001; df=3, 159) had significant influence on oviposition by focal females in the presence of *V. unguiculata.* The interaction between species and plant architecture (F= 2.55, P=0.007, df=9, 159) was significant.

Post hoc analysis revealed that highest oviposition on bean pods and lowest on old leaves of *D. lablab* in all the four ladybird species (Table 2). In case of *V. unguiculata,* highest oviposition was recorded on young leaves and lowest on old leaves in all ladybird species. The maximum oviposition was recorded by C7 while minimum by Pd (Table 2).

(C) Effect of aphid alarm pheromone

The results of two-way ANOVA revealed that oviposition by all ladybirds varied significantly with the species (F= 11.45; P=0.001; df=3, 79) and crushed + intact aphids combination (F= 33.30; P=0.001; df=1, 79). The interaction between species and combination (F= 2.93, P=0.005, df=3, 79) was significant.

The females of all ladybirds laid significantly higher number of eggs in presence of crushed aphid paste with the same intact aphid as compared to the presence of only intact aphid. The influence on oviposition was species-specific. Post hoc analysis revealed that the oviposition was maximum by C7 followed by Ms, Ct and Pd (Fig. 2).

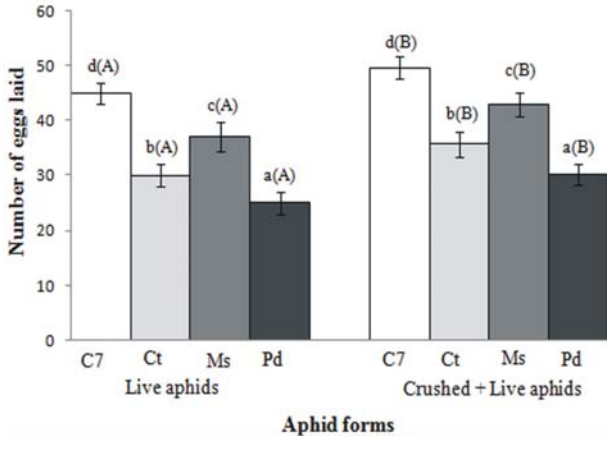

Fig. 2. Mean (±SE) numbers of eggs laid in 24 h by 10 day old female ladybirds (n = 10) in 14.5 × 1.5 cm Petri dishes in the presence of *A. pisum* in two different forms.

Value are Mean±SE.

For each aphid forms, small and capital alphabets (placed in parentheses) represent comparison of means between different focal females within and between aphid forms, respectively. Values followed by different alphabets show significant differences amongst means of a species.

DISCUSSION

The present study revealed that oviposition by females of these ladybird species (C7, Ct, Ms and Pd) was significantly influenced by the aphid-host plant complexes, plant morphology and aphid alarm pheromone. Females showed varied oviposition preference when provided with different aphid-host plant complexes. *Aphis gossypii-L. vulgaris* and *A. craccivora-D. lablab* were preferred more than the same aphids on different host plants. While considering plant architecture, maximum oviposition was recorded on bean pods and young leaves. Addition of crushed aphids enhanced oviposition. Of all species tested, C7 and Ms oviposited maximum eggs as compared to Ct and Pd in all the treatments.

In case of aphid-host plant complexes, maximum oviposition was recorded on *L. vulgaris* followed by *C. grandis* while minimum on *S. melongena* containing *A. gossypii*. This suggests that probably the alkaloids present in *L. vulgaris* infested aphid species are more favourable for oviposition by ladybirds as compared to *S. melongena* which presumably produce deterrent effects on the oviposition. Another possible reason could be the reduced consumption by ladybirds probably in response to harmful chemicals in body contents of *A. gossypii* taken from *S. melongena.* A combination of positive (nutritive) and negative (toxic) tritrophic effects may account for these results. When feeding on plants that contain toxic metabolites, aphids may accumulate these compounds and become toxic to their predators (Canard, 1977; Malcolm, 1990). Ladybirds often reduce consumption of aphids containing such substances, potentially maintaining the ingested toxins below lethal thresholds and ensuring their survival (Pervez & Omkar, 2004). For example, Francis *et al*. (2001a,b) demonstrated that *Myzus persicae* reared on *Brassica napus*, *B. nigra*, and *Sinapis alba*, plants rich in glucosinolates, were less suitable as prey for *Adalia bipunctata*. Similarly, Pratt *et al*. (2008) found that *Brevicoryne brassicae* reared on diets with elevated sinigrin levels had a more detrimental effect on *A. bipunctata* than on *Coccinella septempunctata*. Other studies have also reported adverse effects on ladybird development and reproduction when aphids were reared on resistant plant varieties (Rice & Wilde, 1989; Martos *et al*., 1992).

The *Aphis craccivora-Dolichos lablab* complex appears to be more preferred by ladybirds for oviposition compared to the *A. craccivora-Vigna unguiculata* complex. This supports the idea that prey preference in ladybirds is influenced not only by aphid traits but also by the host plant on which aphids are reared (Omkar & Bind, 1998; Griffin & Yeargan, 2002a,b; Seagraves, 2009). Recognition of specific host plants enhances ladybird performance and survivorship (Walker & Jones, 2001; Rodrigues *et al*., 2010). Thus, species-specific plant compounds play a vital role in attracting ladybirds to aphid patches by facilitating both qualitative and quantitative prey assessment (Schaller & Nentwig, 2000; Griffin & Yeargan, 2002a,b; Omkar & Bind, 1998).

Maximum oviposition was recorded on bean pods of *D. lablab* and young leaves of *V. unguiculata* than on tendrils and old leaves of both the plants. The possible reason for this could be that bean pods and young leaves have relatively soft texture, more sap and nutrition which enables rapid multiplication of aphid colonies whereas old leaves are devoid of sap and have rough texture (Mechaber *et al*., 1996). Though tendrils are soft, nutritious and ladybirds were able to grasp the tendrils and forage more efficiently for the aphids than on glossy leaves (Hodek *et al*., 2012), their thread-like shape possibly does not permit the ladybirds to oviposit on them. The present study is consistent with the results of Klausnitzer & Klausnitzer (1986) who found that most of the ladybirds prefer young leaves for oviposition as they provide high quality resources. Young or fast-growing leaf tissue also correlates positively with larval growth and performance for galling insects and leaf-feeders (Craig *et al*., 1989; Bachtold *et al*., 2013). Architectural traits are known to regulate the search paths of predators (Ferran & Deconchat, 1992; Frazer & McGregor, 1994). By modifying predator mobility, plant structure can also affect predator's residence time or searching efficiency (Carter *et al*., 1984; Kareiva & Perry, 1989). Plant architecture determines the availability of spatial refuges, *i.e.* the proportion of the prey population immune to attacks by the predator/natural enemies (Pimentel, 1961; Gardner & Dixon, 1985; Freese, 1995) and also influences predation risk (Lambret *et al*., 2018). Thus on a single host at different locations like leaves, tendrils, or on the bean pods, the aphids were found. Similar findings were also reported in plant-feeding predatory bugs *Anthocoris nemoralis* (Fabricius) and *Orius insidiosus* (Say) (Gardner & Dixon, 1985; Richards & Schmidt, 1996), which display distinct oviposition preference for specific plant species and sites within the plants. This shows the influence of plant architecture on the fitness of adult ladybirds and their offspring and also on plant acceptability and suitability for oviposition by the ladybirds.

The oviposition was higher when crushed aphids were added with the live aphids. During crushing, the injured aphids release a secretion (aphid alarm pheromone) that gives signal to the ladybirds that these aphids were previously encountered by the predators as this pheromone is released only at that time when aphids are eaten by larvae or adults (Nakamuta, 1991; Derridj *et al*., 1996; Hatano *et al*., 2008; Pettersson *et al*., 2005). Insects exhibit a variety of volatile alarm pheromones to indicate the presence of predators (Verheggen *et al*., 2008). In a series of olfactometer experiments, it was found that adult *C. septempunctata* are able to distinguish between aphid-infested and non-infested plants using olfactory cues (Ninkovic *et al*., 2001). It is likely that the adaptive significance of this pheromone increases the ability of the predators to search the immediate area intensively and locate their prey. Also, sharing the prey killed by another larva benefits the first instars to greatly increase their probability of surviving to the next instars (Derridj *et al*., 1996). It is also found that aphids produce less alarm pheromones when reared singly than in aggregations or when exposed to the odour of other active colonies (Verheggen *et al*., 2008).

Consequently, the present study establishes that oviposition in these ladybird species was greatly influenced by the aphid host-plant complexes, plant architecture and aphid alarm pheromone that strongly impact their population dynamics. More research on mechanisms behind oviposition decisions and reproduction will help to identify specific plant characteristics that influence the decision-making process of ladybirds with respect to oviposition and how these decisions shape the outcome of biological control. Field trials will reveal the possible impact of such tri-trophic interactions investigated under laboratory conditions.

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