



Research Article

Effect of sensitization on the orientation response of *Cotesia plutellae* females towards the odour of cruciferous host plant and host larval body extracts

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ABSTRACT: The importance of odour learning in host habitat and host selection is well demonstrated in many insects. In this present study using *Cotesia plutellae* Kurdjumov as a model, we examined the capacity of naïve *C. plutellae* females to learn and orient towards the odour of cruciferous host plant, host larval body extracts of *Plutella xylostella* (L.), larvae reared on different host plants in a 'Y' tube olfactometer by repeated exposure. The acquired capability to recognize an odour by repeated exposures (sensitization) to a particular odour produced a strong decline in orientation time of wasps to the odour source. The decline in orientation time at 5th exposure level was at least 55% and 36%, respectively, for virgin and gravid females to HPLE odours in relation to first exposure level. Whereas the HLBE odours elicited 49% and 51% decline in orientation time, respectively in virgin and gravid females compared to 1st exposure level. Briefly, the gravid females oriented much faster toward larval body odours compared to host plant odours; while, virgin females were more attracted and rapidly oriented to host plant odours compared to larval body odours, signifying some synomonal / kairomonal substances are involved in influencing the orientation. The rapid orientation response observed for various infochemical extracts demonstrate that *C. plutellae* upon sensitization can respond to the chemical signals of most preferred odour in a host plant-herbivore complex associated with cruciferous crop ecosystem.

KEY WORDS: Sensitization, *Cotesia plutellae*, *Plutella xylostella*, Brassicaceae, host plant extracts, larval body extracts, Y-tube olfactometer, RM-ANOVA, learning, orientation time.

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INTRODUCTION

Diamondback moth (DBM), *Plutella xylostella* (L.) (Lepidoptera: Plutellidae), is a cosmopolitan pest on cruciferous vegetables throughout the world (Talekar and Shelton, 1993). In India, the damage caused by DBM to Cole crop vegetables was 52–56% in Shillong region (Sachan and Gangwar, 1990), while in South-east Asia; major outbreaks of *P. xylostella* reportedly caused more than 90% crop losses (Verkerk and Wright, 1996). It thrives under extremely varying climatic conditions prevailing in different parts of India. The solitary larval endoparasitoid, *Cotesia plutellae* Kurdjumov, (Hymenoptera: Braconidae) effectively minimizes the crop loss under field conditions (Sarfrac *et al.*, 2005). The present work describes how the orientation behaviour of female wasps could be modified by repeated exposure to an odour source. The ability to learn odours that are associated with hosts may help the parasitoids to detect subtle differences between these cues and other non-profitable cues (Turlings *et al.*, 1995) and experiencing an odour signal through learning process without a reward (real host) is called sensitization.

Potting *et al.* (1999) showed that *C. plutellae* uses plant volatiles in its in-flight searching behaviour, which gets modified by its experience with plant materials. The natural odours encountered by parasitoids in their natural environment are both complex and variable mixtures. Plants may mediate many of the interactions between herbivores and their insect parasitoids, which increase or decrease the effectiveness of natural enemies (Cortesero *et al.*, 2000). Several studies demonstrate the consequence of odour learning and increased parasitic potential (Turlings *et al.*, 1989; Kester and Barbosa, 1991; Agelopoulos and Keller, 1994; Kester and Barbosa, 1994; Potting *et al.*, 1997; Vos *et al.*, 1998; Geervliet *et al.*, 1998a; Geervliet *et al.*, 1998b; Potting *et al.*, 1999; Wang *et al.*, 2004) in the genus *Cotesia*. However, the larval parasitoid *C. plutellae* has received little attention on this aspect.

Few authors have reported the host location behaviour of *C. plutellae* and the arrestment response of female wasps emerging from hosts feeding on different plant cultivars (Bogahawatte and Van Emden, 1996; Jiang *et al.*, 2001). The work by Potting *et al.* (1999) describes the

importance and details of pre-flight experience of host plant volatiles by *C. plutellae* and associated changes in the foraging behaviour. However, information on the effect of repeated exposure and associated behaviour modification in orientation response of *C. plutellae* females is scanty. Therefore, the present investigation was aimed to demonstrate, how sensitization of *C. plutellae* females modifies the orientation response time (ORT) of the wasp towards the odour stimuli? by repeatedly exposing them to different cruciferous host plants and the larval body odours of *P. xylostella* reared on these host plants.

MATERIALS AND METHODS

Insects

The host insect, diamondback moth was reared at $26 \pm 2^\circ\text{C}$ on cabbage and cauliflower leaves in open tray rearing method described by Seenivasagan (2001). The nucleus culture of *C. plutellae* was obtained from National Bureau of Agriculturally Important Insects, Bangalore, and then subsequently reared on the second and third instar larvae of *P. xylostella* in the Biological Control Laboratory, Indian Agricultural Research Institute (IARI) at $27 \pm 1^\circ\text{C}$, $70 \pm 5\%$ RH, 10L: 14D photoperiod. Adults were provided with 10% sucrose *ad libitum*, opened raisin and pollen grains as food source.

Host plants

The following cruciferous host plants of DBM, *viz.*, cabbage - *Brassica oleracea* var. *capitata* (Golden acre), cauliflower - *Brassica oleracea* var. *botrytis* (Pusa Snowball K-1), broccoli - *Brassica oleracea* var. *italica* (Pusa KTS-1), knol-khol - *Brassica caulorapha* (White Vienna), Brussels sprout - *Brassica oleracea* var. *gemmifera* (Hilds Ideal), kale - *Brassica oleracea* var. *alboglabra* (Red Russian Kale) and mustard - *Brassica juncea* (Pusa Bold) were grown in the research farm of Indian Agricultural Research Institute (IARI) during Oct-Jan season. The varieties of the host plants were grown in discrete experimental plots of 2 x 2m size with the application of recommended fertilizers. The leaves were picked from host plants 45 days after sowing to culture DBM and for preparation of leaf extracts.

Preparation of extracts and orientation experiments

The host plant leaf extracts (HPLE) and the host larval body extracts (HLBE) were prepared as described by Seenivasagan *et al.* (2009). To study the orientation response of parasitoids 1% of HPLE and HLBE was used with the solvent hexane as control. The orientation response and behaviour of 2-3 day-old virgin and gravid females of *C. plutellae* was investigated in a borosil glass Y-tube olfactometer of 20x20x20 cm size with 1.5 cm inner diameter. Acclimatized naïve females, *i.e.*, those that were

fed only with 10% honey, kept under dark conditions overnight and not exposed to any of the test odours were used for experiments. A blower with a regulator was used to generate and blow charcoal filtered and humidified air inside the experimental arena @ 75–150 ml / min. The bioassay room had a 40W fluorescent bulb as the light source with the temperature of $26 \pm 2^\circ\text{C}$ and $65 \pm 5\%$ relative humidity in a thermostatically controlled environment.

A single parasitoid was released at the stem of the olfactometer and the time taken by the parasitoid to select and reach the arm containing the 50 μl of treatment odour (extract odour) source on Whatman #1 filter paper strip (30 x 10 mm size) was observed. The other arm released the control (solvent hexane 50 μl) odour. Each wasp was allowed to walk freely inside the 'Y' tube. When a wasp moved more than 10 cm into one of the arms and reached the odour source, it was recorded as making a choice and the time taken by the parasitoid wasp to reach the extract odour source was recorded using a stopwatch in every release at different exposure levels. In any case, the time taken by female wasp which made its first choice to orient towards the control odour was also taken into observation till it reaches back to treatment odour. A new olfactometer was used for every release of naïve parasitoids and the location of the odour stimulus was changed alternately for every release to avoid any biased orientation.

A single wasp was repeatedly exposed for five times to find the effect of sensitization to the odour source for each host plant as well as HLBE extracts. At least 30 minutes were allowed to elapse between two trials of a parasitoid from its first exposure to the subsequent exposure to odour stimulus. Twenty parasitoids were assayed individually to obtain twenty replicates in an experimental trial. The total experimental time was 10 minutes for each wasp in a replicate. The female wasps which didn't exhibit any foraging activity for up to 5 minutes or did not move beyond the fork were discarded and the experiment was repeated with another naïve wasp. Between different experimental trials the olfactometer was washed with 75% ethanol and oven dried at 200°C to remove volatiles from the previous trials. All the experiments were conducted between 0800–1600 hrs of the day.

Statistical analysis

The data obtained in Y-tube olfactometer experiments on orientation response time (seconds) of parasitoid females to various host plant and larval body extracts were subjected individually to One way-Repeated Measures Analysis of Variance (RM-ANOVA) in SPSS 10.0 software (SPSS Inc, IL, Chicago, USA). The difference between subsequent exposure levels was compared using Tukey's HSD (Honestly Significant Difference) with 99% confidence interval by applying Bonferroni Correction factor. Paired

t-test (SPSS Inc.) was used to compare the difference in ORT at each exposure level between virgin and gravid females.

RESULTS AND DISCUSSION

The experiments on sensitizing the parasitoid wasps by repeatedly exposing them to a particular odour revealed that, repetitive exposure modified the orientation response time and behaviour of wasp to the sensitized odour. We observed that the naïve /unsensitized adult virgin and gravid females of *C. plutellae* took longer time to reach the odour source compared to sensitized wasps as a result of sensitization induced modification in the orientation response after perceiving the odour plume. A marked decline in the orientation time to reach the odour source by both virgin and gravid parasitoid females indicated the effect of sensitization. The mean time taken (in seconds) by virgin and gravid females to orient towards HPLE odours declined significantly with increasing exposure levels (Fig. 1). One way RM-ANOVA on ORT of both virgin and gravid *C. plutellae* females to HPLE odour revealed significant differences between different exposure levels (Table 1). Repeated exposure to a particular odour augmented the sensitization of responding wasp, which was translated into rapid orientation towards the experienced or learned odour. The virgin females showed rapid orientation to all the HPLEs upon increasing exposure levels. It has been reported that the response of *C. plutellae* females to plant derived cues was significantly increased after an oviposition experience on PHC and exposure only to a host damaged leaf (Potting *et al.*, 1999). This increased propensity to make oriented flights is due to increased sensitivity or by associative learning process.

Analysis by paired *t*-test revealed that there was a significant difference ($P < 0.01$) between virgin and gravid females to a particular extract odour. However, the orientation time at 5th exposure (Exposure-V) was not significant for cauliflower and broccoli extracts ($P > 0.05$, $df = 19$). At 3rd exposure level the ORT of gravid *C. plutellae* to Knol-khol extract was not significant from virgin females (Table 2). Virgin females of *C. plutellae* exhibited more rapid orientation toward HPLEs with increasing exposure levels compared to gravid females. Although gravid *C. plutellae* females exhibited rapid orientation toward host plant odours with repetitive exposure probably by increased sensitization, a significant decline in ORT was observed than in virgin females for some extracts. At the 5th exposure level, leaf extracts of cabbage, knol-khol, Brussels sprout, kale and mustard elicited slower, but significant orientation responses from gravid females (see Fig. 1). Among the extracts tested, Brussels sprout, kale and mustard elicited slower orientation responses from *C. plutellae* at all exposure levels. The observed results indicate that the chemical signals perceived by the female parasitoid wasp from the infochemical source of the cruciferous host plants were more excitatory to virgin females than gravid females. Further, one or more synomone compounds could be involved in sensitizing the responding females with increased exposure levels. In addition, Paul and Yadav, (2002) have opined that the retention of natural enemies in the released area and the increased foraging success can be ensured by exposing the natural enemy to host or host plant-related chemical cues before releases.

Table 1. Results of one-way repeated measures ANOVA on orientation response time of virgin and gravid females of *C. plutellae* to cruciferous host plant leaf extracts and host larval body extracts at different levels of exposure

Host plants used for rearing DBM larvae and preparation of extracts	Host plant leaf extracts			Host larval body extracts		
	Virgin female	Gravid female	<i>P</i> (sig.) Value	Virgin female	Gravid female	<i>P</i> (sig.) Value
	F _(4,76) value	F _(4,76) value		F _(4,76) value	F _(4,76) value	
1. Cabbage	930.11	445.48	<0.001	482.19	388.91	<0.001
2. Cauliflower	730.45	1061.52	<0.001	321.84	883.55	<0.001
3. Broccoli	1537.10	332.33	<0.001	465.93	868.43	<0.001
4. Knol-khol	890.49	457.62	<0.001	370.36	729.17	<0.001
5. Brussels sprout	564.26	343.09	<0.001	596.82	506.53	<0.001
6. Kale	521.22	446.08	<0.001	816.31	613.38	<0.001
7. Mustard	232.68	934.44	<0.001	271.44	448.75	<0.001

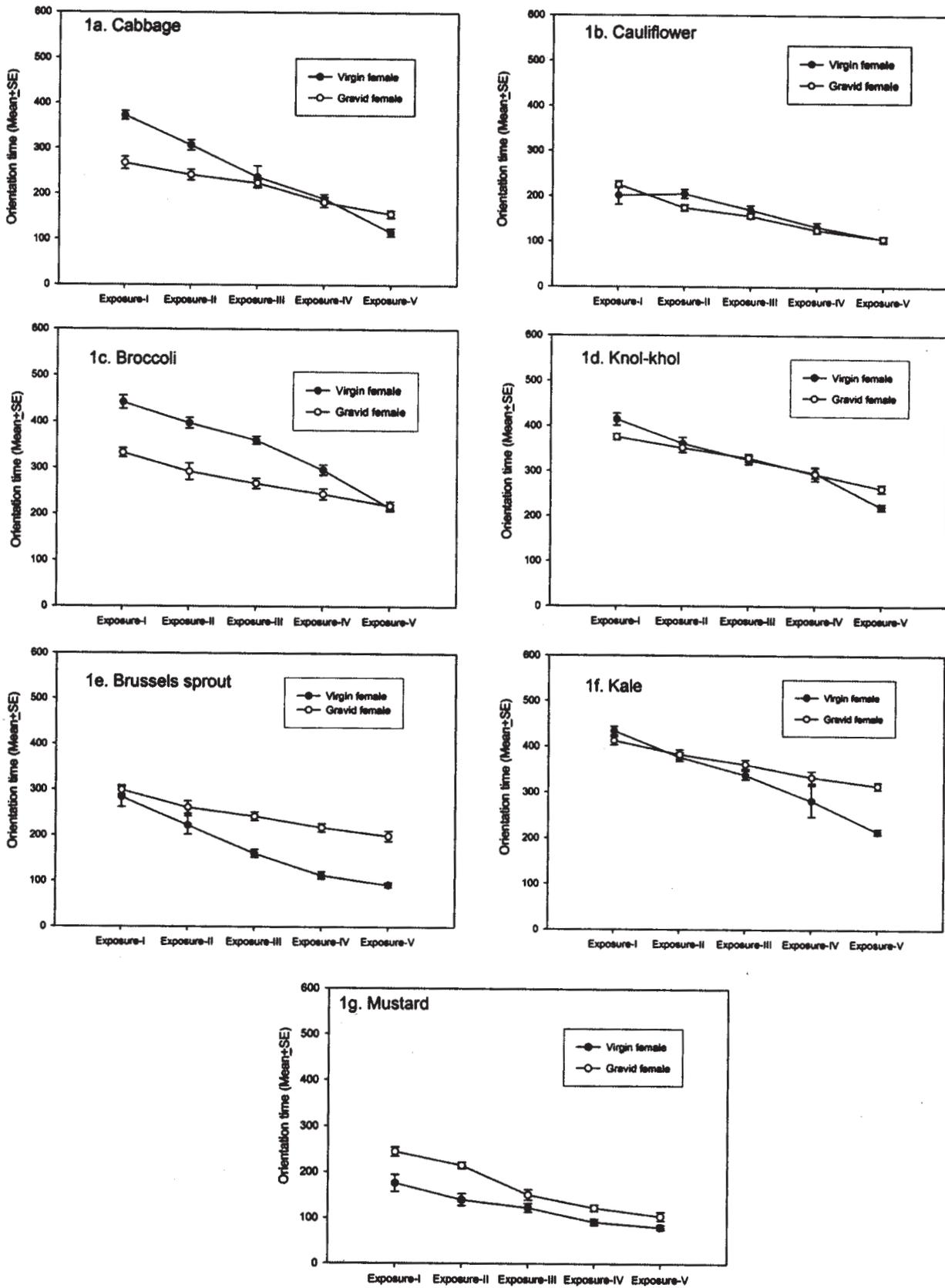


Fig. 1. Change in the orientation response time (seconds) of virgin and gravid *Cotesia plutellae* females upon repeated exposure to the odour of host plant leaf extracts. Values of orientation time with standard error bars on the trend lines are mean of 20 replicates ($n = 20$) for each exposure level ($P < 0.001$)

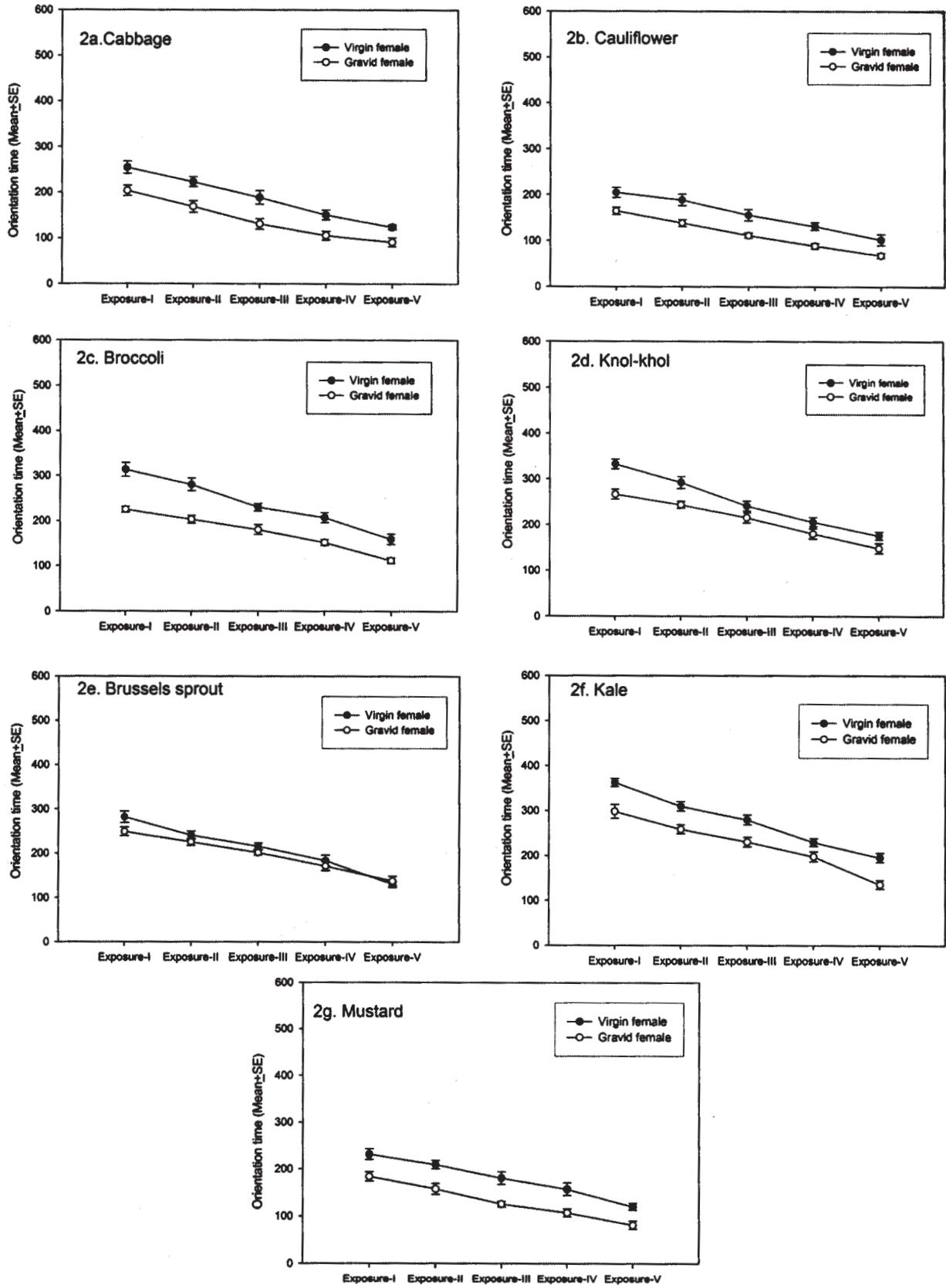


Fig. 2. Change in the orientation response time (seconds) of virgin and gravid *Cotesia plutellae* females upon repeated exposure to the odour of host larval body extracts. Values of orientation time with standard error bars on the trend lines are mean of 20 replicates (n = 20) for each exposure levels ($P < 0.001$)

Table 2. Results of paired t-test to compare the orientation response time (n=20) between virgin and gravid females of *Cotesia plutellae* to hexane extract of host larvae and cruciferous host plants

Host plants used for rearing the DBM larvae and preparation of extracts	Sensitization/ Exposure level	Difference in orientation response time (seconds) between virgin and gravid females of <i>Cotesia plutellae</i>					
		Host plant leaf extracts			Host larval body extracts		
		Mean \pm S.E value	t ₍₁₉₎ value	P (sig. 2)	Mean \pm SE value	t ₍₁₉₎ value	P (sig. 2)
Cabbage	Exposure-1	104.60 \pm 4.03	25.94	P<0.01	50.75 \pm 3.88	13.07	P<0.01
	Exposure-2	64.95 \pm 3.60	18.03	P<0.01	54.10 \pm 3.38	16.00	P<0.01
	Exposure-3	13.65 \pm 5.31	2.57	P<0.02	58.05 \pm 4.66	12.45	P<0.01
	Exposure-4	7.85 \pm 2.75	2.85	P<0.01	44.90 \pm 3.34	13.43	P<0.01
	Exposure-5	-40.15 \pm 2.49	-16.12	P<0.01	32.30 \pm 1.91	16.90	P<0.01
Cauliflower	Exposure-1	17.55 \pm 2.26	7.76	P<0.01	40.05 \pm 3.12	12.83	P<0.01
	Exposure-2	30.85 \pm 3.24	9.53	P<0.01	50.65 \pm 2.49	20.34	P<0.01
	Exposure-3	13.30 \pm 2.51	5.31	P<0.01	44.50 \pm 3.03	14.70	P<0.01
	Exposure-4	7.45 \pm 2.47	3.02	P<0.01	42.60 \pm 2.46	17.31	P<0.01
	Exposure-5	-0.65 \pm 1.94	-0.34	P = 0.74NS	33.65 \pm 2.24	15.01	P<0.01
Broccoli	Exposure-1	109.30 \pm 3.67	29.78	P<0.01	88.30 \pm 3.60	24.50	P<0.01
	Exposure-2	105.00 \pm 3.01	34.89	P<0.01	77.40 \pm 2.99	25.86	P<0.01
	Exposure-3	93.80 \pm 3.55	26.41	P<0.01	27.30 \pm 2.35	11.61	P<0.01
	Exposure-4	52.65 \pm 4.03	13.08	P<0.01	55.00 \pm 2.98	18.46	P<0.01
	Exposure-5	-4.20 \pm 2.56	-1.64	P = 0.12NS	47.35 \pm 2.73	17.32	P<0.01
Knol-Khol	Exposure-1	38.95 \pm 3.62	10.76	P<0.01	65.65 \pm 4.47	14.69	P<0.01
	Exposure-2	9.70 \pm 2.65	3.67	P<0.01	48.60 \pm 3.62	13.43	P<0.01
	Exposure-3	-4.25 \pm 2.10	-2.02	P = 0.06NS	25.60 \pm 3.34	7.66	P<0.01
	Exposure-4	-23.00 \pm 3.03	-7.58	P<0.01	54.05 \pm 2.60	20.79	P<0.01
	Exposure-5	-41.45 \pm 2.32	-17.86	P<0.01	2260 \pm 6.25	3.62	P<0.01
Brussels sprout	Exposure-1	-15.30 \pm 4.84	-3.16	P<0.01	32.95 \pm 4.11	8.02	P<0.01
	Exposure-2	-39.10 \pm 5.57	-7.02	P<0.01	14.95 \pm 2.73	5.48	P<0.01
	Exposure-3	-81.35 \pm 2.14	-37.97	P<0.01	14.35 \pm 2.18	6.59	P<0.01
	Exposure-4	-104.75 \pm 2.62	-40.00	P<0.01	12.45 \pm 3.61	3.45	P<0.01
	Exposure-5	-107.45 \pm 2.82	-38.12	P<0.01	-7.50 \pm 3.05	-2.46	P<0.02
Kale	Exposure-1	21.80 \pm 2.37	9.19	P<0.01	64.60 \pm 4.13	15.63	P<0.01
	Exposure-2	-5.60 \pm 2.25	-2.49	P<0.02	51.40 \pm 2.82	18.21	P<0.01
	Exposure-3	-23.20 \pm 1.97	-11.80	P<0.01	49.05 \pm 3.41	14.38	P<0.01
	Exposure-4	-51.65 \pm 8.20	-6.30	P<0.01	31.40 \pm 3.26	9.63	P<0.01
	Exposure-5	-100.30 \pm 2.37	-42.30	P<0.01	60.05 \pm 2.55	23.57	P<0.01
Mustard	Exposure-1	-68.35 \pm 4.64	-14.73	P<0.01	47.65 \pm 3.69	12.90	P<0.01
	Exposure-2	-74.75 \pm 2.91	-25.68	P<0.01	51.55 \pm 2.40	21.47	P<0.01
	Exposure-3	-28.35 \pm 3.23	-8.79	P<0.01	54.85 \pm 3.23	17.00	P<0.01
	Exposure-4	-30.70 \pm 2.30	-13.34	P<0.01	49.70 \pm 3.15	15.77	P<0.01
	Exposure-5	-24.15 \pm 2.49	-9.70	P<0.01	38.90 \pm 2.15	18.09	P<0.01

The HLBE odours elicited intense antennation and rapid orientation toward the source in gravid females. In contrast to the orientation response observed for HPLEs, gravid females exhibited faster orientation compared to virgin females (Fig. 2). Significant difference between exposure levels in orientation response of virgin and gravid females of *C. plutellae* was revealed by one-way RM-ANOVA for all the extracts of DBM larva reared on various host plants (Table 1). In the present study, with increasing acquaintance to host plant / host related cues, the orientation response of *C. plutellae* increased towards the reliable odour source at much faster rate compared to unsensitized wasps. Similar results were reported odour of respective host larval body extracts. Values of orientation time with standard in *Diadegma* sp. by Seenivasagan *et al.* (2003) to the host kairomone odours. This is possibly due to the increased sensitivity of odour perception mechanism or tuning of peripheral olfactory receptors, similar to the one reported for tortricid moth after prolonged exposure to plant volatiles (Stelinski *et al.*, 2003).

More rapid orientation by gravid females towards HLBE odour irrespective of the host plant on which they had been reared depicts the specificity and profitability of HLBE odour to the foraging gravid females for parasitization, which might not have influenced virgin females to act in the same manner, although there was a gradual decline in ORT with increasing exposure levels. Vet and Dicke (1992) reported that herbivore produced kairomone generally evoked strong and congenially fixed responses, while responses to plant volatiles were more plastic. In each exposure level, the gravid females of *C. plutellae* exhibited rapid orientation than virgin females. However, the ORT was slightly higher for the HLBE derived from Brussels sprout ($t = 2.46$, $df = 19$, $P < 0.024$) than virgin females at 5th exposure level (Table 2). The increased orientation of wasps with increasing exposure to HPLE and HLBE odours agrees with the findings of Eller *et al.* (1992) who reported that females of *Microplitis croceipes* (Cresson) which had a pre-flight experience with plant-host-complex (PHC) prior to testing exhibited a higher percentage of orientation towards odour source than inexperienced females. In a choice situation a single experience was sufficient to establish a preference for the PHC experience in the insects and repeated experience resulted in preference and the degree of preference tended to increase with the number of experiences.

In conclusion, our present investigation suggests that in addition to sensitization induced modification in orientation responses (*i.e.*, the experience gained without real host insect), the potential effects of chemical constituents in the leaves' waxy layer, larval cuticle, internal lipids and airborne cues for their role in tri-trophic interaction of host plant-herbivore-parasitoid complex mediated by synomone and kairomone components should also be taken into consideration when evaluating the

foraging success of natural enemies like *C. plutellae*. Breeding of cruciferous crop varieties with broad leaves and abundant wax surfaces to release large number of attractive chemical signals into the parasitoid's foraging environment would enhance the efficiency of larval parasitoids and thus improve the biological control of diamondback moth.

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