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Orientation and behavioural responses of *Cotesia plutellae* Kurdjumov (Hymenoptera: Braconidae) to cruciferous host plants and host larval body extracts

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ABSTRACT: The foraging activity of a parasitoid is highly influenced by the chemical cues released from the host plants and their potential hosts in a cropping system. The larval parasitoid *Cotesia plutellae* parasitizes the diamondback moth (DBM), *Plutella xylostella* most efficiently in cruciferous crop ecosystems throughout the world. In this study, we have evaluated and report the effect of hexane extracts of certain selected host plants and larvae of DBM reared on these host plants on the odour preference and orientation behaviour of *C. plutellae* using multi-armed olfactometer and Y-tube olfactometer. The orientation response indicated that host larval body extracts were more attractive and stimulatory to host seeking females than host plant leaf extracts at 1% concentration. Gravid females responded in relatively larger numbers to both host larval body and host plant leaf extracts compared to virgin females. These extracts could be used to enhance the foraging ability of *C. plutellae* to contain the menace of diamondback moth in cruciferous crop fields.

KEY WORDS: *Cotesia plutellae, Plutella xylostella*, orientation response, host plant and host larval body extracts, foraging ability, olfactometer, integrated pest management

INTRODUCTION

The diamondback moth, *Plutella xylostella* (L.), is the most serious pest of cruciferous crops and completely cosmopolitan in distribution. It causes extensive damage to plants of the family Cruciferae belonging to the genus *Brassica* all over the world (Talekar and Shelton, 1993). It has developed high level of resistance to almost all groups of insecticides. In the last three decades, largely due to improvements in analytical techniques and an increased desire to reduce the reliance on broad-spectrum insecticides, there has been augmented interest in behavioural manipulations for pest management (Foster and Harris, 1997). The behaviour of natural enemies is greatly influenced by the diverse semiochemicals present in a given ecosystem. Plant genotype influences the quality and quantity of allelochemicals released in any ecosystem by the plant and also the infochemicals released by the host insects. In many instances, these allelochemicals change with the age / stage of the plants, by which the interaction between plants-host insects and the natural enemies is greatly modified (Paul and Yadav, 2002).

The behaviour modifying chemicals found in the ecosystem play a dominant role in the process of host selection and acceptance by insect natural enemies. The survival of natural enemies is dependant on the interaction between the trophic levels and their ability to exploit various elements that exist in these complex ecosystems. Dynamic continuum of chemical signals present in the ecosystems is utilized by the natural enemies to find food, mate and also to locate, identify and exploit suitable hosts for their progeny (Paul, 2003). Host-derived stimuli are most reliable indicators of the presence of hosts, but they may be hard to detect at long distances, where as plant derived stimuli are assumed to be more detectable (Vet *et al.*, 1991). Volatile semiochemicals mediate a wealth of interactions between organisms from different trophic levels, including phytophagous insects, their parasitoids and predators (Vet and Dicke, 1992).

Some of the previous studies aimed to investigate the role of volatiles in host searching behaviour of *C. plutellae* focused on the foraging behaviour of this parasitoid under field conditions. For example, findings like *C. plutellae* preferred the odour of *Brassica* type (Blue lake cabbage) on which they had developed (Bogahawatte and Van Emden, 1996), volatiles from herbivore damaged and mechanically damaged plants were more attractive to *C. plutellae* (Potting *et al.*, 1999), host searching behaviour was increased at herbivore damaged areas in the leaves (Shiojiri *et al.*, 2000a; Shiojiri *et al.*, 2000b), and the host parasitism rate was

five-fold higher on Chinese cabbage than that on common cabbage (Jiang *et al.*, 2001) elucidate the role of plant volatiles or herbivore induced plant volatiles in enhancing the foraging efficiency of this specialist parasitoid. But information on the specific strength of volatiles emitted by these plants or herbivores which are more stimulatory and behaviourally reliable to the foraging parasitoid is lacking.

Further, literature available on the effect of extracts of host plant leaves and host larvae and their influence on the foraging and orientation behaviour of *C. plutellae* is very limited. So, in the present investigation we have made an effort by screening a range of concentration of extracts of selected host plants of DBM and larval body extracts to determine the biologically most reliable and readily detectable concentration of extract stimulus to the host searching parasitoids. The main objectives of our study were to screen and determine biologically most stimulating concentration of the various extracts using multiple choice experiments and evaluate the odour preference and orientation behaviour of *C. plutellae* to these extracts in dual choice experiments which would help to enhance the foraging ability of parasitic wasps.

MATERIALS AND METHODS

Host plants

The cruciferous host plants of diamondback moth were grown in the research farm of Indian Agricultural Research Institute (IARI), New Delhi, during October-January season. Breeder seeds of popular varieties of 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 obtained from National Seeds Corporation (NSC), New Delhi, Horticultural Research Station (HRS) - Katrain (Himachal Pradesh) and Division of Vegetable Science, IARI, New Delhi. The host plants were grown in the nursery and after 25-30 days, seedlings were transplanted in discrete experimental plots of 4 x 4m size with the application of recommended fertilizers suitable for local conditions. The leaves were picked from host plants at active vegetative stage for rearing the diamondback moth and preparation of leaf extracts.

Host insects

The host insect, diamondback moth, was maintained on cabbage / cauliflower leaves in the culture room at 27±1° C, 60-70% RH, and 10L:14D photoperiod in open trays at the Biological Control Laboratory, IARI, New Delhi as described by Seenivasagan (2001). The leaves were washed in water, wiped dry and fed to the host larvae. The culture trays were thoroughly swabbed with 0.2% sodium hypochlorite solution to avoid contamination. The larvae were reared on cruciferous host plant leaves in open trays of 27 x 13 x 3.5 cm size and covered with a black muslin cloth. When the matured larvae pupated, the pupae were collected and kept for adult emergence in a Perspex glass cage (30 x 30 x 30 cm) with a muslin cloth sleeve. Adult moths were provided with 10% glucose / honey solution. Fresh leaves kept in a 50 ml vial of water were presented to the female moths for oviposition. The moths laid creamy white eggs on both dorsal and ventral sides of leaves. After 24-48 hours of oviposition and depending upon the egg density, the older leaves were replaced with fresh leaves. The freshly hatched larvae were transferred to new trays with fresh host plant leaves to initiate the next generation of host insects.

Parasitoids

The nucleus culture of *C. plutellae* was obtained from the Project Directorate of Biological Control (PDBC), Bangalore. One/two pairs of parasitoid wasps were kept overnight for mating in a perplex glass cage (30 x 30 x 30 cm size) and offered with a counted number of host larvae (DBM) for parasitization for about 24–48 hours. The adult parasitoids were fed with 10% glucose / honey solution and opened resins. Parasitized larvae were transferred to new trays after 48hrs and reared following the normal procedure till the formation of parasitoid pupae in silken cocoons on the leaf surface. The cocoons were collected and stored in a refrigerator at 10°C till further use. Upon emergence, the adults were examined and sexed for further multiplication and use in experiments.

Extracts of host plant leaves and host larval body

Host plant leaf extracts (HPLE) were made by overnight immersion of 30g (fresh weight) of undamaged leaves of cruciferous host plants in 300 ml of hexane. The host larval body extract (HLBE) was prepared by immersing uniformly grown late 3rd instar/early 4th instar larvae weighing ca.1g (fresh weight) (reared on various host plants) overnight in 30 ml of HPLC grade hexane and further extracted in a thermostatically controlled water bath shaker (Haake 220SWB) for an hour at 28°C and later for 15-20 minutes at 50°C with gentle rotation. The HPLE and HLBE were filtered through Whatman #1 filter paper, dehydrated with 1-3 g of anhydrous sodium sulphate (Na_2SO_4) for an hour and passed through a column having 2 cm internal diameter with 100 gram of degassed silica gel (60-120 mesh). Separate columns were used for individual extracts. The eluted filtrate was concentrated to 500µl by passing charcoal filtered air (N_2) through a tube at room temperature. The concentrated residue was pipetted out to a

new vial and collected further by rinsing the container with another 500µl of HPLC grade hexane. This preparation constituted the 100 % extract (mother liquor) and stored at -20°C in a deep freezer for bioassay.

Experimental set up

Multi-armed olfactometer experiments

The dosage response of *C. plutellae* to various host plants and host larval body extracts was investigated under multiple-choice conditions using a six-armed borosil glass olfactometer (internal arena of 20 cm diameter, 7.5cm height, covered at the top) in a room at 27±1°C, 65±5% RH with a 40W fluorescent lamp as the source of light. A stock solution of 1% was prepared from the mother liquor of each extract. Further concentrations (0.1, 0.01, 0.001 and 0.0001%) were prepared in hexane (HPLC grade, Merck) by serial dilutions in decadic steps.

The extracts were applied @ 50µl onto a Whatman No.1 filter paper strip (30 x 10 mm size) and after the evaporation of the solvent, they were placed individually inside the arm/stimulus tube, 1.5cm ID located at a distance of 10cm from the periphery of the central arena attached to the olfactometer by a grooved joint. The other end of the arm was closed with hexane washed and oven dried cotton plugs. One strip of filter paper with 50µl hexane served as control. The arms of the olfactometer and air inlet tubes were connected to the central arena with a blower which blew the charcoal filtered air into each arm @ 7.15ml/min.

A group of six cold immobilized gravid females (2-3 days old) was released at the centre of the olfactometer and covered using a glass plate having air outlet with a sieve/ wire mesh at the centre to prevent their escape. When the wasps recovered, the blower was switched on and the behaviour of wasps to choose the most reliable and preferred concentration of odour source was observed for 10 minutes by counting the number of parasitoid wasps visiting the filter papers treated with different concentrations of individual plant extract / larval extracts in different arms, which constituted one replicate. Five such replications were made for each extract entirely with naïve female wasps. Assays with different extracts were performed separately with naïve wasps on different days during 0700-1700 hrs of photo phase. Between every trial / replicate, a new olfactometer was used along with stimulus tubes. The olfactometer and stimulus tubes were washed with ethanol/ hexane thoroughly and heated at 200°C for an hour in a hot air oven to remove any remaining odour of extracts used in the previous trial.

Y-tube olfactometer experiments

The experimental conditions are mostly similar to that of multi-armed olfactometer. A Borosil® glass Y-tube olfactometer (20x20x20 cm size, 1.5 cm internal diameter) was used to assess the odour preference of *C. plutellae* under dual-choice conditions. The odour stimulus of 1% concentration was used in these experiments as it was most stimulating to the foraging parasitoids. A single parasitoid was released at the stem of the olfactometer and the response of female parasitoids (virgin & gravid) to either of the odour source was recorded by counting the number of parasitoids opting for the host plant / host larval odour against n-hexane (control) odour applied @ 50µl on Whatman #1 (30x10 mm size) filter paper strip. Twenty numbers of parasitoids used in a single experimental trial constituted one replicate and repeated for five times with different groups of parasitoid wasps for every host plant and host larval body extracts. The wasps which didn't exhibit any orientation or foraging activity up to five minutes were discarded and the experiment was set up again with another naïve female wasp. The location of the odour stimulus was changed alternately for every release and for every release a new Y-tube was used. Between every trial, the tubes were washed with ethanol/hexane and dried in an oven at 200°C to remove any possible odours of extracts used in previous trials.

Statistical Analysis

The number of parasitoid wasps responding to various concentration of host plant leaf extracts and host larval body extracts in multiple choice experiments were log transformed [log(x+1)] and analyzed by 2-way ANOVA (SPSS 10.0, GLM procedure). The difference between the means of two treatments within a group was compared by LSD. The observations on dual-choice tests, i.e., the numbers of females making orientation to choose between two odours (solvent control vs host plant/host larval body extract) were compared by Chi-square test in a 2x2 contingency table with Yates correction (Sokal and Rohlf, 1981) assuming 50:50 distribution in the probability of orientation to select the preferred odour source. The mean difference between the orientation response of *C. plutellae* to individual extracts was sorted out by LSD test in 1-way ANOVA, while the significant differences in the response between virgin and gravid females of *C. plutellae* to host plant / host larval body extracts were determined by Mann-Whitney U-Test.

RESULTS AND DISCUSSION

The gravid females of *C. plutellae* showed a significant increase in activity to cauliflower and mustard leaf extracts ($F=5.20$, $df=6$, $P<0.001$). Both the extracts attracted significantly increased number of wasps with increasing concentrations in a dose-dependent manner compared to control odour (Fig. 1). Although other cruciferous host

plants presented a dose-dependent increase in wasp activity, they were not significant. The odour preference of gravid *C. plutellae* females in terms of mean parasitoid response (MPR) was highest to cauliflower followed by mustard (F=17.96, df=5, P<0.001). Although increased parasitoid activity was recorded at lower concentrations compared to solvent control, the preference for most stimulating concentration behaviourally relevant for the parasitoid, asserts the profitability of odour source for the location of suitable host for parasitization by the females. The in.teraction effect of concentrations with different extracts was not significant (F=0.33, df=30, P <0.998).

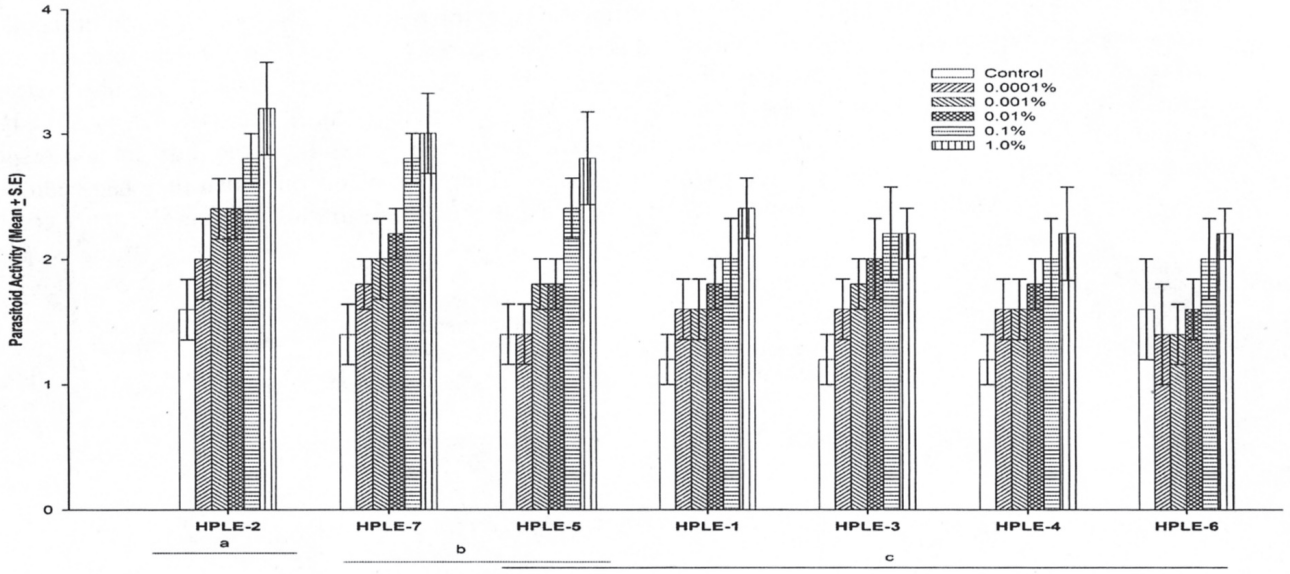

Fig. 1. Dose response (Mean±S.E) of gravid females of C. *plutellae* in multi-armed olfactometer to extracts (HPLE 1-7) from undamaged leaves of Cabbage, Cauliflower, Broccoli, Knol-knol, Brussels sprout, Kale and Mustard at different concentrations. Data are averages of five replicates (n=5; P<0.001); in each replicate six wasps were assayed. HPLE in the X-Axis connected by a bar with different letter are statistically significant

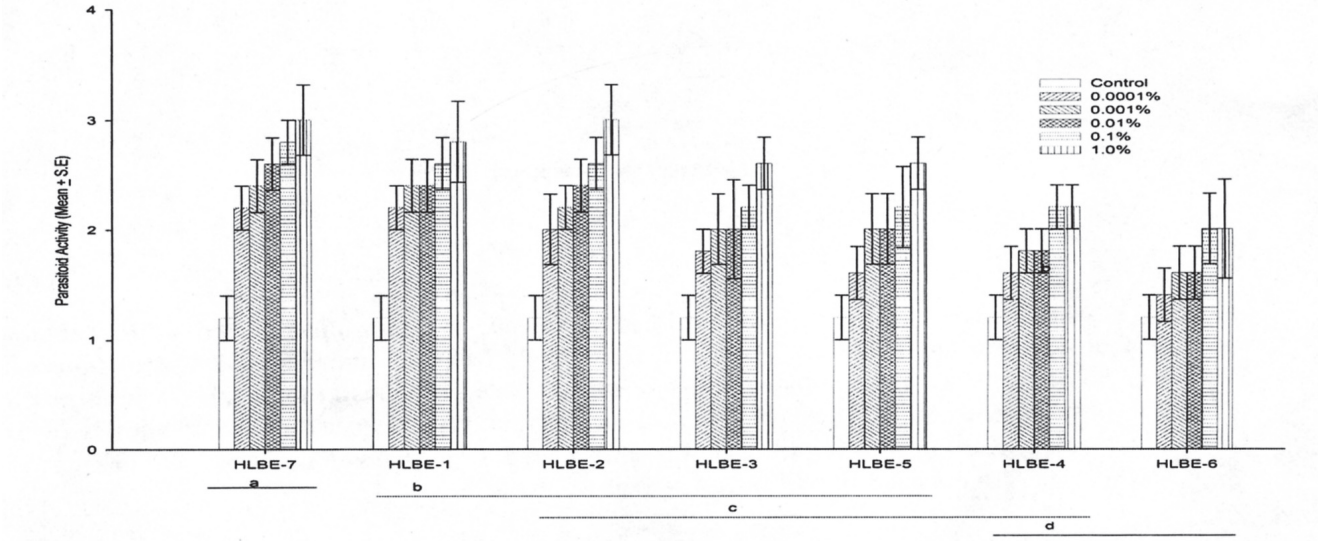

Fig. 2. Dose response (Mean±S.E) of gravid females of C. *plutellae* in multi-armed olfactometer to larval body extracts (HLBE 1-7) of diamondback moth reared on Cabbage, Cauliflower, Broccoli, Knol-knol, Brussels sprout, Kale and Mustard. Data are averages of five replicates (n=5; P<0.001); in each replicate six wasps were assayed. HBLE in the X-Axis connected by a bar with different letter are statistically significant

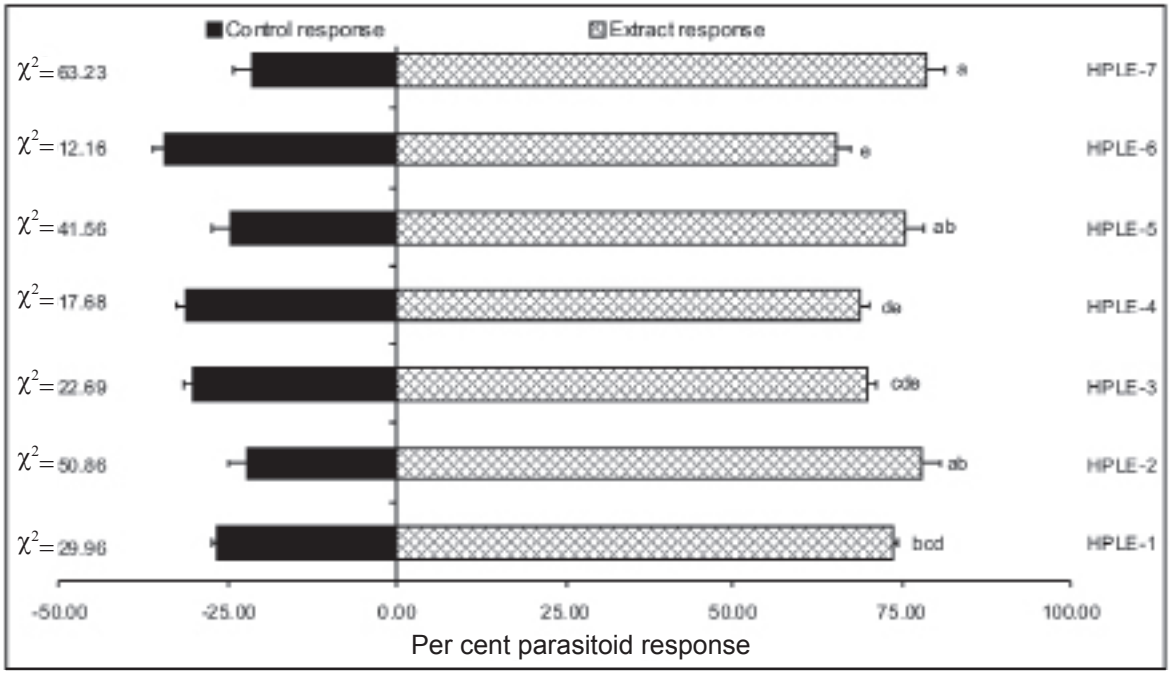

Fig. 3. Orientation response of virgin females of *C. plutellae* in Y-tube olfactometer to leaf extracts (HPLE 1-7) of Cabbage, Cauliflower, Broccoli, Knol-khol, Brussels sprout, Kale and Mustard at 1.0% concentration. Data are per cent response of five replicates (n=5; P<0.001, χ^2 test); in each replicate 20 wasps were used. Error bars on mean per cent orientation with the same letters are not significantly different

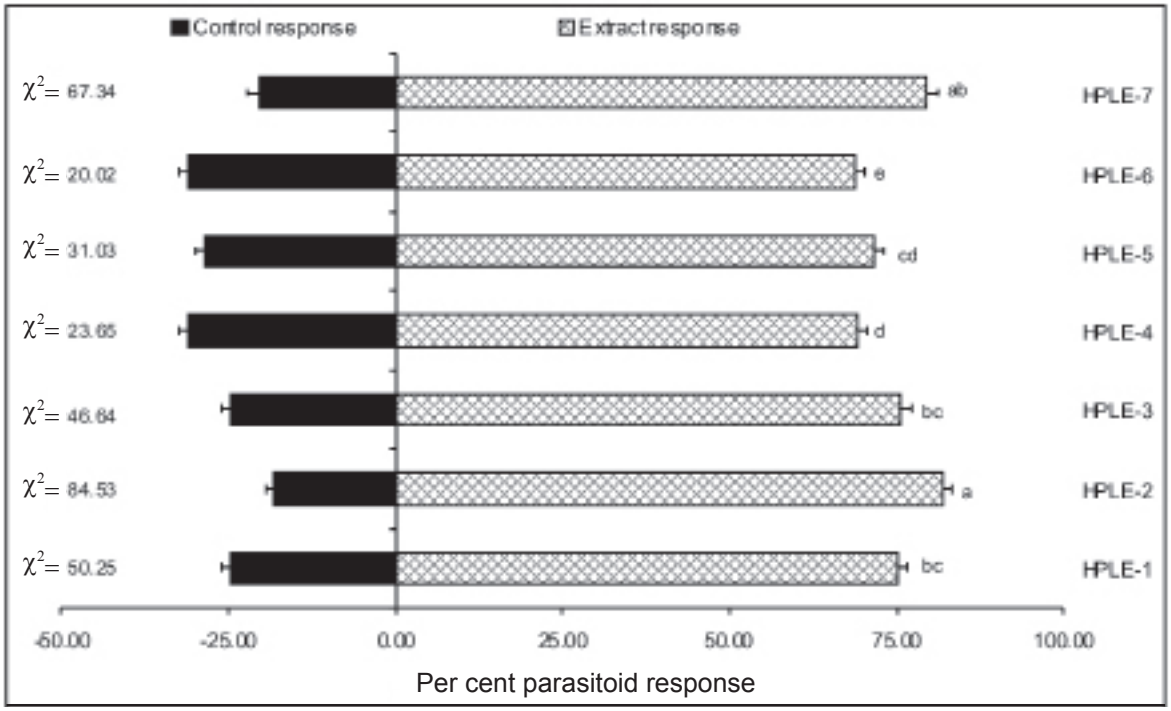

Fig. 4. Orientation response of gravid females of *C. plutellae* in Y-tube olfactometer to leaf extracts (HPLE 1-7) obtained respectively from the undamaged leaves of Cabbage, Cauliflower, Broccoli, Knol-khol, Brussels sprout, Kale and mustard at 1.0% concentration. Data are per cent response of five replicates (n=5; P<0.001, χ^2 test); in each replicate 20 wasps were used. Error bars on mean per cent orientation with the same letters are not significantly different

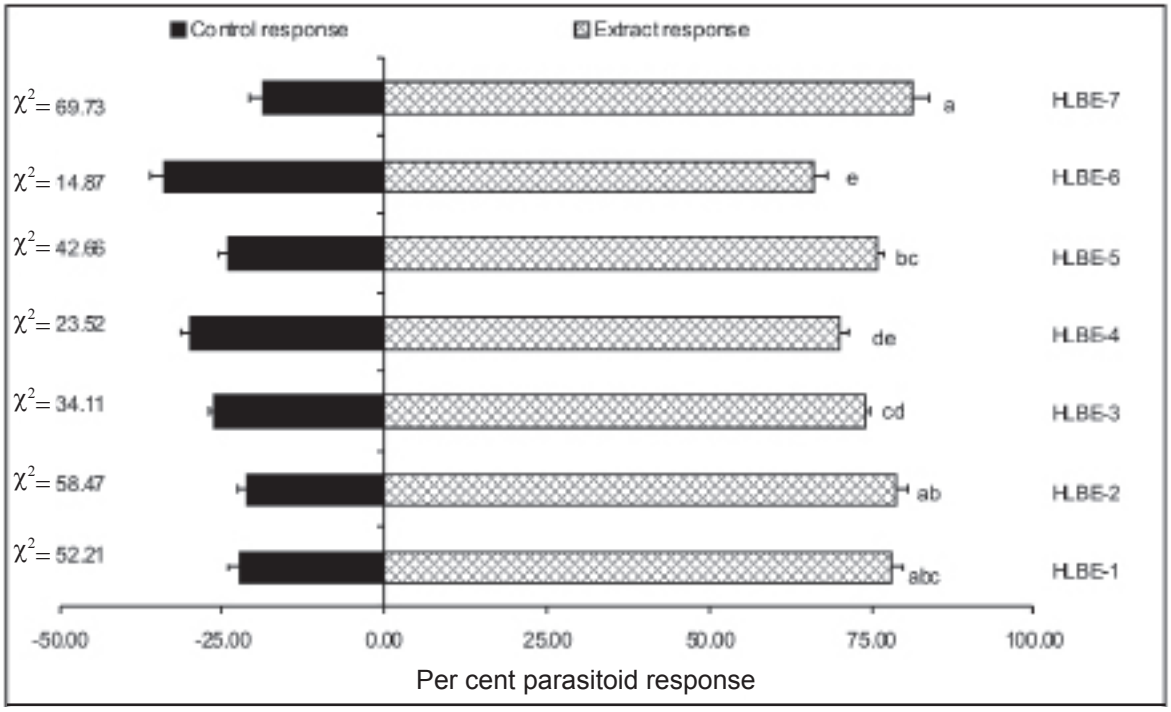

Fig. 5. Orientation response of virgin females of *C. plutellae* in Y-tube olfactometer to larval body extracts (HLBE 1-7) of DBM reared on Cabbage, Cauliflower, Broccoli, Knol-khol, Brussels sprout, Kale and Mustard at 1.0% concentration. Data are per cent response of five replicates (n=5; P<0.001, χ^2 test); in each replicate 20 wasps were used. Error bars on mean per cent orientation with the same letter sare not significantly different

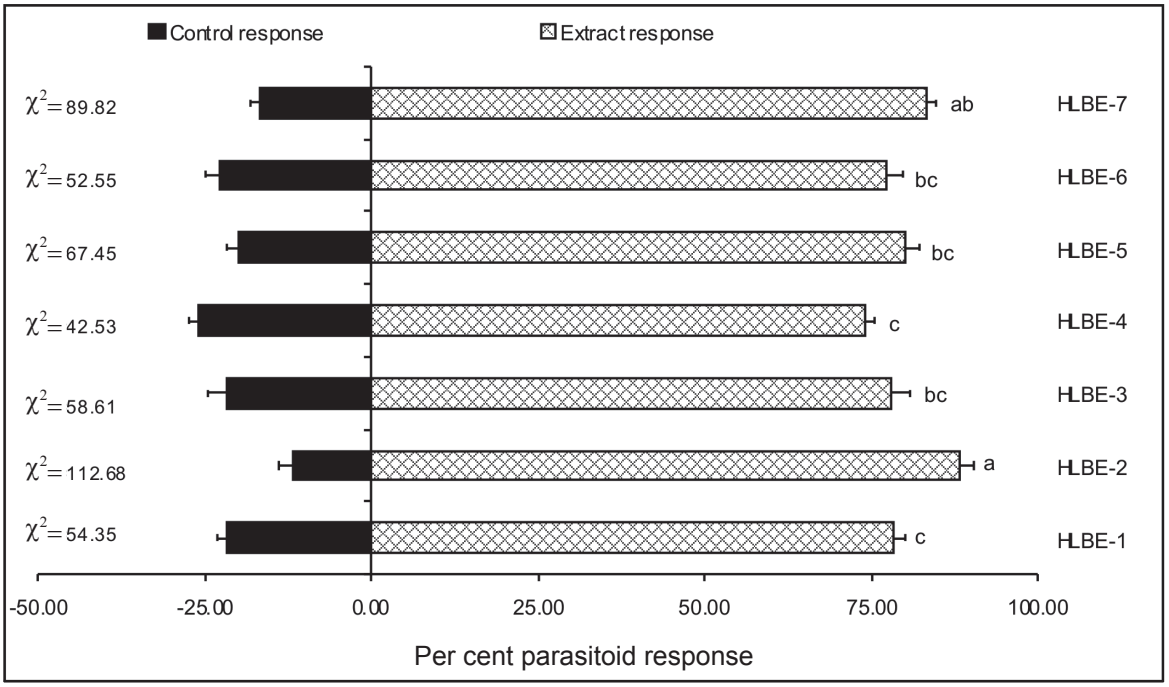

Fig. 6. Orientation response of gravid females of *C. plutellae* in Y-tube olfactometer to larval body extracts (HLBE 1-7) of DBM reared on Cabbage, Cauliflower, Broccoli, Knol-khol, Brussels sprout, Kale and Mustard at 1.0% concentration. Data are percent response of five replicates (n=5; P<0.001, χ^2 test); in each replicate 20 wasps were used. Error bars on mean per cent orientation with the same letters are not significantly different

The activity of *C. plutellae* was significantly increased by the host larval body extract (HLBE) of larvae reared on mustard followed by cabbage, cauliflower and broccoli (F=6.11, df=6, P<0.001). The stimulatory effect on *C. plutellae* was prominent at 1% dose of all the extracts; however, mustard elicited the strongest response, significantly different from cabbage, cauliflower, broccoli and Brussels sprout fed larval extracts (F=25.66, df=5, P<0.001). At lower concentrations, extracts from the larvae reared on broccoli, knol khol and kale did not elicit significant parasitoid activity compared to control (Fig. 2). The interaction effect of concentrations with different extracts was not significant (F=0.34, df=30, P <0.998). Our observations on slightly elevated orientation response to few extracts are supported by the Loke and Ashley (1984) who found that the mated, gravid, 1-3 days old females of *C. marginiventris* exhibited the most intense responses to potential sources of kairomones. In general, irrespective of the host plants on which they had been reared, the MPR of *C. plutellae* was increased when encountering higher concentrations of larval odours compared to solvent control.

In the dual-choice bioassays carried out in Y-tube olfactometer, all the host plant leaf extracts attracted significantly more number of parasitoids than the respective controls (χ^2-test; 50:50 distribution). Among the extracts tested, mustard (79%) and cauliflower (78%) elicited significantly increased orientation response from virgin females compared to kale extract to which the least response (66%) was observed (F=5.87, df=34, P<0.001). The order of preference of virgin females to HPLE odours from the highest to lowest than the respective controls was mustard > cauliflower > Brussels sprout > cabbage > broccoli > knol khol > kale (Fig. 3). Virgin females showed more preference for host plant extracts which lead them to the host habitats, where they can encounter their mates. Several parasitoids and predators are known to use volatile infochemicals that are emitted by herbivore-plant complexes when searching for their host and prey (Takabayashi and Dicke, 1996; Dicke *et al.*, 1998; Turlings and Fritzsche, 1999). In the present study, cauliflower leaf extract attracted significantly higher number of gravid females at much higher rate (82%) followed by mustard (80%) than the respective controls. Knol-khol and kale extract were found to be least attractive (69%) to females (F=6.92, df=34, P<0.001). The order of response from the highest to the lowest response was cauliflower > mustard > broccoli > cabbage > Brussels sprout > Knol khol > kale (Fig. 4).

Host larval body extracts in general attracted higher number of wasps compared to host plant leaf extracts. The preference of virgin females of *C. plutellae* to the HLBE was significantly higher compared to the respective control stimuli. HLBE derived from diamondback moth larvae reared on mustard and cauliflower elicited 81% and 79 %, significantly increased response, respectively (F=8.62, df=34, P<0.001), and the wasps exhibited least preference (66%) to the odour of kale extract. The order of orientation response from the highest to the lowest response was mustard > cauliflower > cabbage > Brussels sprout > broccoli > knol khol > kale (Fig. 5). It is evident from these results that the necessity and ability of gravid females to orient towards the odours of host larval extracts to locate and find suitable hosts and their possible hideouts for parasitization. Parasitoids may use non-specific plant volatiles as long range cues to lead them to the general arena where they are likely to find herbivores feeding on a plant. Once they have located such an area, wasps may rely on more specific cues such as host frass, silk, and salivary secretions (Elzen *et al.*, 1987; Turlings *et al.*, 1991; Steinberg *et al.*, 1993; Cortesero *et al.*, 1997; Rose *et al.*, 1997).

The cumulative response of *C. plutellae* females as evidenced by the total number of wasps responding to a particular extract's odour revealed that host larval body extracts were more attractive than host plant leaf extracts. Gravid females responded in relatively higher numbers to both host larval body and host plant leaf extracts compared to virgin females as indicated by Mann-Whiney U-test. Significantly larger number of females were attracted to HLBE obtained from cauliflower (88%) followed by mustard (83%) and showed least preference (74%) for the knol-khol extract (F=5.23, df=34, P<0.001). The order of odour preference displayed by the gravid females from the highest to the lowest compared to the respective control stimuli was cauliflower > mustard > Brussels sprout > broccoli > cabbage > kale > Knol khol (Fig. 6). In the present investigation, *C. plutellae* females responded in increased numbers to HLPE and HLBE of cauliflower and mustard exhibiting highest degree of preference. This may be because the herbivore produced chemicals are obviously the most reliable source of information about herbivore presence and identity (Steinberg *et al.*, 1993).

In the olfactometer bioassays the parasitoid females after reaching the odour source deprived of larvae made a return to the release point in search of host larvae for oviposition. Sometimes they attempted stinging on the odour impregnated filter paper which corroborates the findings by Potting *et al.* (1999) that the female *C. plutellae* tended to return to the same site after encountering host related products / cues or after oviposition.

In India, the practice of growing *Brassica juncea* as a trap crop around Cole crop fields offers effective control of diamondback moth. In this study, the results are convincing that, in dual choice experiments to a large extent the parasitoids apparently exhibited their order of preference for HPLE as well as HLBE odours to a particular odour plume

against the control odour. Among the extracts evaluated at 1% concentration, both cauliflower and mustard odours were more stimulatory to foraging parasitoids. Further experiments are needed to enhance the efficiency of *C. plutellae* under semi-field and open-field conditions which would help in understanding the influence of these extracts if applied over the plant foliage. Such attempts would be eco-friendly and reduce the use of insecticides as a component of integrated pest management.

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