Effects of Postemergence Experience on Searching and Landing Responses of the Insect Parasitoid, *Cotesia congregata* (Say) (Hymenoptera: Braconidae), to Plants

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Postemergence experience with one of six plant species, in the presence of the host larva, modified the searching response of reproductively mature females of Cotesia congregata (Say) to these plants in at least one of three ways: (1) an increased response to the plant experienced at emergence, (2) an increased response to other plants, or (3) an inhibited response to other plants. Landing and searching responses were differentially affected by postemergence experience. For example, postemergence experience with tobacco (a common plant) in the presence of the host larva induced a landing preference for this plant over parsley (a novel plant) but did not affect searching responses to either plant, whereas experience with parsley and the host larva induced an increased searching response to parsley but a landing preference for tobacco. Differential effects of postemergence experience may reflect the type of stimuli involved in searching or landing and may have adaptive significance.

KEY WORDS: postemergence learning; cross-induction; foraging behavior; *Cotesia congregata* (Say); Braconidae; Hymenoptera.

INTRODUCTION

Parasitoid foraging behavior is generally regarded as a complex and catenary process involving different stimuli at each step (Vinson, 1975, 1976) and is

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based on genetically fixed, as well as learned behaviors (Lewis *et al.*, 1990). Similarly, learning may involve a series of separate experiences that are modified with each subsequent experience and then integrated or refined over time (Vet *et al.*, 1990). If so, earlier experiences may directly or indirectly affect the occurrence or outcome of subsequent experiences, particularly if each separate experience involves different stimuli and affects only some components of foraging behavior.

To date, most reports of learning in insect parasitoids have involved associative learning of olfactory stimuli by reproductively mature females in the presence of their host or host by-products (e.g., Arthur, 1966, 1967; Vet, 1983; Vet and van Opzeeland, 1984; Drost et al., 1986, 1988; Lewis and Tumlinson, 1988; Sheehan and Shelton, 1989; Wardle and Borden, 1989; Turlings et al., 1989). In addition, parasitoid foraging may be modified by exposure to habitat cues prior to adult emergence (Thorpe and Jones, 1937; Vinson et al., 1977; Vet, 1983; Luck and Uygun, 1986) or, more likely, immediately following adult emergence (Wardle and Borden, 1986; Herard et al., 1988; Kester and Barbosa, 1991a). Most studies of associative learning or conditioning in insects have considered only how an organism's response to a particular habitat or plant changes as a result of previous experience with that habitat or plant. However, exposure to habitat- or plant-derived stimuli may also modify an insect's response to other, previously unexperienced habitats or plants, as well. This phenomenon, known as "cross-induction," has been reported for a few saprophagous or phytophagous species (Jaenike, 1983, 1988; Papaj and Prokopy, 1986; Papaj et al., 1989) and, although assumed to occur in insect parasitoids (Vet et al., 1990), has not been investigated previously.

In related work with *Cotesia congregata* (Say) (Hymenoptera: Braconidae), a gregarious larval endoparasitoid of the tobacco hornworm, *Manduca sexta* L. (Lepidoptera: Sphingidae), and other larval sphingids, we found that exposing females to a novel plant in the presence of their host larva immediately following adult emergence induced an increased searching response to this novel plant but an inhibited searching response to an inherently attractive plant (Kester and Barbosa, 1991a). We hypothesized that the primary function of postemergence learning was to retain emergent parasitoids on the plant on which they had undergone development and, thus, to encourage assortative mating. However, since these experiential effects extended beyond the preovipositional period, we also hypothesized that postemergence learning could affect the foraging behavior of reproductively mature females, either directly, by modifying some components of foraging, or indirectly, by increasing the likelihood that first ovipositional experiences would occur on the plant experienced by emergent females.

In this paper, we report our further investigations of postemergence learning in C. congregata. We tested two hypotheses: (1) that postemergence experience with one plant modifies the responses of C. congregata to other plants and (2)

that postemergence experience differentially affects searching and landing response to the plant experienced by *C. congregata*. Since landing responses under natural conditions most likely reflect the outcome of a series of decisions based on stimuli provided by different plant species, we measured landing responses in two- or three-way choice trials in a flight chamber. In this manner, we also controlled for other variables that affect the flight response of *C. congregata*. For example, even naive females are strongly attracted to most plants and the proportion of females responding to flight stimuli is apparently affected by abiotic factors such as temperature, humidity, and barometric pressure (Kester, unpublished). In contrast, searching responses were tested in no-choice trials since searching responses to individual plant species are, most likely, based on stimuli provided by direct contact with a particular plant.

MATERIALS AND METHODS

Inherent Searching Responses of *C. congregata* to Selected Host Plants of Potential Caterpillar Hosts

In this and similar preliminary experiments, we tested the hypothesis that *C. congregata* females would show inherently different searching responses to both host and nonhost plants. In surveying a broad array of plants, we identified plants which elicited strong, moderately strong, and weak searching responses for inclusion in the experiments described below. Plants selected for this representative experiment were those on which potential sphingid hosts would be most typically encountered under field conditions in Maryland (Kester and Barbosa, 1991b). Searching responses were assayed as described below.

Insects. Parasitoids used in the first two experiments originated from our stock laboratory colony, which was established in 1983 and has been periodically replenished with individuals emerging from M. sexta feeding on tobacco on several occasions. Parasitoids were reared as described by Barbosa *et al.* (1991) except that parasitoid cocoons were not detached from host larvae and host larvae were fed on a modified version (wheat germ based) of the BioServ hornworm diet (Kemper, unpublished). Hornworm eggs were provided by the Insect Neurobiology and Hormone Laboratory at USDA-ARS, Beltsville, Maryland.

When egression of larval parasitoids was observed, individual hornworms were transferred from rearing cups to clear plastic (150-ml) cups, the lids of which had been streaked with honey. Cohorts of newly emerged adult parasitoids from each of 10 hornworms were retained with their hosts in the clear plastic cups for 30 min–1 h, then released into one of five plastic holding cages. Adult parasitoids were maintained on honey and water. We assume that all females used in the experiments described below were mated since each cohort contained

both females and males, and mating was observed throughout the (24- to 48-h) preovipositional period following eclosion (Kester and Barbosa, 1991a).

Plants. The plants assayed in this experiment represented species in two genera in each of five plant families: Virginia creeper (Vitaceae: *Parthenocissus*), wild grape (Vitaceae: *Vitis*), trumpet creeper (Bignoniaceae: *Campsis*), catalpa (Bignoniaceae: *Catalpa*), wild rose (Rosaceae: *Rosa*), wild cherry (Rosaceae: *Prunus*), willow (Salicaeae: *Salix*), poplar (Salicaeae: *Populus*), tobacco (Solanaceae: *Nicotiana*), and tomato (Solanaceae: *Lycopersicon*).

Leaves were randomly collected from wild and cultivated plants at the Tobacco Research Farm in Upper Marlboro (Prince George's County), Maryland, and held in water until their use about 1 h later. Leaves were collected from healthy plants near the terminal portion of the plant (herbs) or stems (vines and trees) and were free of apparent insect damage or disease. Tobacco and tomato plants were cultivated without the use of pesticides.

Searching Assay. Two-day-old females of C. congregata were held individually in 1-dr glass vials with cork stoppers and held for 2-6 min before being tested. To control for possible leaf area effects, we assayed the searching responses of these females to uniformly sized disks of leaf (0.8 cm in diameter) cut from the upper third of each leaf with a cork borer. Each disk was held on a piece of filter paper for 2 min and then introduced into the vial with forceps. Total time spent searching on the leaf disk within a 2-min period was measured for each female. "Searching" was defined as active antennal palpation on any area of the leaf disk. The 2-min test period was established on the basis of our preliminary work. Individual females were tested on one plant only and were not returned to their original holding cages.

Experimental Design and Analysis. This experiment was designed as a oneway analysis of variance (ANOVA) to test the effect of plant species on searching time. The analysis was performed using SAS GLM (SAS Institute, 1985); all assumptions for ANOVA were met. Resulting means for each plant were compared using the PDIFF option in SAS GLM and judged significant when P < 0.005.

Effect of Postemergence Experience with One Plant on the Searching Responses of *C. congregata* to Other Plants

In this experiment, we tested two alternative hypotheses: (1) postemergence exposure to a nonpreferred plant will induce an increased searching response to this plant but will not affect searching responses of *C. congregata* to other plants, and (2) postemergence exposure to a nonpreferred plant will induce an increased searching response to this plant but will also affect searching responses of *C. congregata* to other plants.

Plants. The plants included in this experiment include several which were

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identified as moderately or weakly attractive in the preliminary experiment described above: catalpa, tobacco, tomato, and wild cherry. Two other plants identified as moderately attractive in another preliminary assay were also included: honeysuckle (Caprifoliaceae: *Lonicera* sp.) and "nicandra" (Solanaceae: *Nicandra physaloides*). Honeysuckle was included because it is a host plant of a common day-flying sphingid, *Hemaris diffinis* (Boisduval) (Hodges, 1971), and nicandra was originally included to permit comparison of the major alkaloid subgroups within the Solanaceae; tobacco and tomato are representative of the other two groups (Bell and Charlwood 1980). With the exception of nicandra, all plants assayed in this experiment are abundant native or introduced species in Maryland.

One hour prior to their use, catalpa, wild cherry, and honeysuckle leaves were randomly collected from plants growing on the University of Maryland campus and held in water. Tobacco, tomato, and nicandra leaves were collected from plants cultivated without pesticides in the University of Maryland greenhouse. Preliminary studies indicated that *C. congregata* showed similar searching responses to tobacco or tomato leaves collected from healthy greenhouse-grown or field-grown plants.

Postemergence Exposure to Plants. Unless otherwise noted, parasitoids were handled as described for the preceding experiment. As soon as the first adult parasitoids within each cohort emerged, we introduced torn leaves from one of the six plant species into the clear plastic cups in which each cohort was held. Leaves were retained in the closed cups for about 3 h to ensure that adults within a single cohort, typically emerging over a 2.5- to 3-h period, received at least a 30-min exposure to leaves immediately following emergence. After the 3-h exposure period, parasitoids were introduced into plastic holding cages; cups containing hornworm hosts and leaves were removed from the cages an hour later. Each treatment group, consisting of three or four parasitoid cohorts exposed to the same plant at the same time $(\pm 1$ h of first exposure to leaves) was held in a single cage. Two-day-old females were randomly chosen from their holding cages and their searching responses to one of the six selected plants were assayed, as described above.

Experimental Design and Analysis. This experiment was designed to test the main and interactive effects of experimental replication (three replications), postemergence experience (one of the six plants or no plant experience), and plant species (six species) on searching time. Prior to analysis, data were transformed by square root (searching time + 0.5) to correct for normality of residuals. The analysis was performed using SAS GLM (SAS Institute, 1985). To determine if postemergence exposure to a specific plant induced a subsequent increased searching response to this plant, we used the PDIFF option in SAS GLM to compare the mean searching time of females exposed to their hosts only (control) on each plant with the mean searching time of females exposed to a particular plant, e.g., mean searching time of control females on tobacco of control females vs mean searching time of females exposed to tobacco and hosts on tobacco. To determine if postemergence exposure to one plant species affected searching responses to other plants, thereby disrupting the inherent rank order of searching responses to the selected plants, interaction contrasts were performed between each plant exposure group and the control group.

Comparison of Searching Responses and Landing Preferences of C. congregata to Selected Plants

In this experiment, we tested the hypothesis that inherent searching and flight responses of *C. congregata* to plants would differ. We compared the searching responses of naive females (exposed only to their hosts for 3 h following adult emergence) from two different strains of *C. congregata* to three plants. Two of these plants, tobacco and tomato, are common host plants of *M. sexta* and the third, cauliflower, is the nonhost herb species that elicits the strongest inherent searching response in *C. congregata* of all nonhost herbs we have assayed. Females from our "U.M." and "WYE" strains of *C. congregata* were used in this experiment because they differ in their searching responses to tobacco and tomato but show similar landing responses to these plants (Kester and Barbosa, 1991b).

Parasitoids were reared and exposed to their hosts for 3 h following eclosion, as described in the preceding section. Individual females were tested only once and different individuals were used for the searching and flight assays. Searching and flight responses of individual females were assayed 3 days after adult eclosion, when *C. congregata* shows the greatest flight responsiveness (Kester, unpublished) and searching responses are the same as those of 2-dayold females (Kester and Barbosa, 1991a). Searching responses were assayed in no-choice trials using the searching assay described above. Flight responses were assayed using the landing preference assay described below.

Flight Chamber. The flight chamber used in our work is based on a design by M. Keller, University of Adelaide, Australia. It is a "pull"-type chamber constructed of cast acrylic and glass, measuring 203.2 cm in length, 76.2 cm in width, and 76.2 cm in height. Air is pulled through the tunnel by an externally mounted single-speed ($\frac{3}{4}$ -HP) motor equipped with a squirrel cage blower, filtered through a layer of packed straws and double fine-meshed screens before entering the tunnel and then through another set of screens before exiting the chamber. Wind speed is varied by drawing the exiting air through one of several variously sized metal templates, previously calibrated with an anemometer. The chamber is illuminated with two 243.84-cm day-length spectral fluorescent bulbs (GE Chromoline 50) suspended above the tunnel within a wooden frame.

Landing Preference Assay. In landing assays, we used healthy vegetative

plants in pots which were grown in a greenhouse without pesticides and selected for their similar sizes. Prior to each test period, plants were arranged downwind in the flight chamber so that their heights and presentations, relative to the upwind release point, were similar. Plants were then artificially damaged by removing a single 0.8-mm (diameter) disk from each plant with a cork borer near the terminal portion of a fully expanded leaf in such a way that damage sites were at similar heights and positions. Plants were repositioned (left-right) after every five positive landing responses.

Females from each treatment group were randomly chosen from each holding cage and held individually in 1-dr glass vials with cork stoppers for 2–5 min before being released in the flight chamber. The release stage was adjusted so that upon their exit from the glass vials, females would be at the same level as damage sites on the plants. Only first landing choices were recorded, with almost all females landing at or in direct proximity to a damage site. Assays were conducted at 30°C, 55–60% RH, and 0.5 cm/s wind speed.

Experimental Design and Analyses. Main and interactive effects of strain (U.M. or WYE) and plant (tobacco, tomato, or cabbage) on searching time were tested in a two-way ANOVA using SAS GLM (SAS Institute, 1985) and resulting means for each plant within each strain were compared using the PDIFF option in SAS GLM. To evaluate the significance of these pairwise comparisons, the level of significance was adjusted using a Boneferoni's method value (P = 0.05/3 comparisons = 0.016). Landing preferences of females from the two strains for the three plants were compared using a generalized Fisher's exact test (Mehta and Patel, 1983).

Effects of Postemergence Exposure to a Novel Plant on Searching and Landing Responses of C. congregata

On the basis of the results of the preceding experiment, we hypothesized that postemergence experience with a novel plant would affect searching responses and landing preferences of *C. congregata* differently. Parsley was chosen as the novel plant because it elicits the weakest searching response of any nonhost herbaceous species we have assayed. Tobacco was used for comparison for two reasons: it is a very common host plant of moderate attractiveness that elicits a stronger searching response than tomato in two of our three strains but is not preferred for landing. Tobacco and parsley plants were grown from seed in a greenhouse and maintained without pesticides.

As described above, newly emerged parasitoid adults received one of three postemergence experiences: hornworm hosts only, tobacco leaves and hornworm hosts, or parsley leaves and hornworm hosts. Searching responses and landing preferences of 3-day-old adult females from each of the three treatment groups were assayed, as described above. Individual females were tested only once and

different individuals were used in each assay. To permit more direct comparisons of the results of this experiment with the preceding one, we used females from our U.M. strain.

Experimental Design and Analysis. The searching component of this experiment was designed and analyzed as a two-way ANOVA to test the main and interactive effects of postemergence experience (hornworm host only, parsley and hornworm host, or tobacco and hornworm host) and plant species (parsley or tobacco) on searching time. The analysis was performed using SAS GLM (SAS Institute, 1985). Resulting means were compared using the PDIFF option in SAS GLM and evaluated using a Boneferoni's method for adjusting the level of significance [P = 0.05(5)/7 comparisons]. Landing preferences of females from the three treatment groups for tobacco or parsley were compared using a generalized Fisher's exact test (Mehta and Patel, 1983).

RESULTS

Searching Responses of C. congregata to Selected Host Plants

Searching responses of 2-day-old adult females of *C. congregata* with no prior exposure to plants differed significantly with respect to the plant offered (P = 0.0001; 1,50 df). On the basis of the searching responses elicited, these plants could be broadly classified into one of three groups of attractiveness: very attractive (Virginia creeper, wild grape, trumpet creeper, wild rose, and willow), moderately attractive (catalpa, tobacco, tomato, and poplar), or weakly attractive (wild cherry), as shown in Fig. 1.

Effect of Postemergence Experience with One Plant on the Searching Responses of *C. congregata* to This and Other Plants.

The effects of postemergence experience on searching responses to the six plants tested did not differ between the two replications, as indicated by the insignificant three-way interaction of experimental replication, postemergence exposure, and plant assayed (P = 0.9513). Postemergence experience with hosts and one of six selected plants affected the searching responses of 2-day-old females of *C. congregata* to these plants, as indicated by the significant two-way interaction of experimental replication and postemergence experience was significant (P = 0.0112), this result is difficult to interpret. For example, in addition to the type and intensity of postemergence experience or the plant offered, searching responses of *C. congregata* are also affected by

temperature, relative humidity, and slight fluctuations in barometric pressure (Kester, unpublished). Results of the complete ANOVA are shown in Table I.

Plant experience at adult emergence induced at least one of three changes in the searching responses of 2-day-old females of *C. congregata:* (1) an increased response to the plant experienced at emergence, (2) an increased



Fig. 1. Searching responses of *Cotesia congregata* (Say) exposed to their hornworm hosts only following adult emergence. Bars represent the ls mean \pm SE response of five females. Means with different letters are significantly different (P < 0.005). Plants tested were as follows: VAC, Virginia creeper; GRA, wild grape; TPC, trumpet creeper; ROS, wild rose; WIL, willow; CAT, catalpa; TOB, tobacco; TOM, tomato; POP, poplar; and CHE, wild cherry.

 Table I. Results of Analysis of Variance Performed to Test the Effects of Experimental Replication, Postemergence Exposure (to the Hornworm Host Only or to the Hornworm Host and One of Six Plants) on the Searching Responses of Cotesia congregata (Say) to Each of These Six Plants^a

Source of variation	df	F value	P
Experimental Replication	1	19.03	0.0001
Postemergence Exposure	6	1.54	0.1625
Plant Assaved	5	8.26	0.0001
Experimental Replication			
\times Postemergence Exposure	6	2.80	0.0112
Experimental Replication			
× Plant Assayed	5	1.34	0.2463
Postemergence Exposure			
× Plant Assayed	30	3.96	0.0001
Experimental Replication			
× Postemergence Exposure			
× Plant Assayed	30	0.61	0.9513
Error	464		

^aAnalysis was performed using SAS GLM (SAS Institute, 1985); data were transformed by sqrt (searching time + 0.5) prior to analysis to correct for normality of residuals.

response to plants other than the one experienced, or (3) an inhibited response to plants other than the one experienced (Figs. 2A-F). For example, postemergence experience with the hornworm host and wild cherry induced an increased searching response to both wild cherry and tomato and an inhibited response to tobacco and nicandra (Fig. 2F). Likewise, postemergence experience with the hornworm host and catalpa or honeysuckle (Lonicera) induced an increased searching response to the plant experienced by newly emerged females and an inhibited searching response to tobacco (Figs. 2A and D). However, although exposure to hosts and any of the three solanaceous plants (tobacco, nicandra or tomato) did not induce increased searching responses to the plant experienced by newly emerged females or inhibit searching responses to other plants, it did induce increased searching responses to other plants (Figs. 2B, C, and E). For example, postemergence experience with the hornworm host and tobacco induced an increased searching responses to nicandra, tomato, and wild cherry (Fig. 2B), experience with the hornworm host and nicandra induced an increased response to tomato (Fig. 2C), and experience with the hornworm host and tomato induced an increased response to Lonicera (Fig. 2E).

Overall, the cross-induced changes in searching responses of *C. congregata* were not reciprocal and appeared to be unrelated to the taxonomic relatedness of the plants offered, e.g., postemergence exposure with catalpa induced an increased response to wild cherry and an inhibited response to tobacco but exposure to wild cherry did not induce an increased response to catalpa, nor did exposure to tobacco induce an inhibited response to catalpa (Figs. 2A, B, and F). Changes induced by postemergence experience with the hornworm host and catalpa, tobacco, tomato, or cherry caused a disruption of the inherent rank order of searching responses to the six plants tested, as indicated by the significant (P < 0.05) interaction contrasts shown in Table II.

Searching and Landing Responses of *C. congregata* to Tobacco, Cauliflower, and Tomato

Searching responses of 3-day-old adult females of *C. congregata* varied with respect to the strain from which they originated and the plant on which searching responses were measured, as indicated by the significant two-way interaction of parasitoid strain and plant assayed (Table III). Females from the U.M. strain searched as long on cauliflower as they did on tobacco (P = 0.2120) and searched longer on either of these plants than they did on tomato ($P \le 0.0049$), whereas females from the WYE strain searched as long on tomato as they did on tobacco (P = 0.3173) and searched for less time on either of these plants than they did on cauliflower ($P \le 0.0018$) (Fig. 3A). However, landing preferences for cauliflower, tobacco, or tomato did not differ between the strains (P = 0.704), and although females showed no preference for either tobacco or



Fig. 2. Effect of postemergence experience on the searching response of *Cotesia congregata* (Say) to six plants. Females were exposed to their hornworm hosts and to leaves from one of the six plants species, as indicated by each legend, for 4 h immediately following adult emergence and assayed 48 h later. Each bar represents the ls mean \pm SE response of 15–20 individuals. Stars indicate a significant (P < 0.05) difference in the mean response of treatment and control females (exposed only to their hornworm hosts). Overall, postemergence experience modified the inherent rank order of searching responses (see Table II).







Effects of Postemergence Experience in C. congregata

Contrast	df	F value	Р
Catalpa vs control	5	3.55	0.0038
Tobacco vs control	5	2.52	0.0292
Nicandra vs control	5	2.11	0.0640
Honeysuckle vs control	5	2.13	0.0608
Tomato vs control	5	2.98	0.0119
Cherry vs control	5	9.41	0.0001

 Table II. Results of Interaction Contrasts Performed to Test the Effects of Postemergence

 Exposure to One of Six Plants on the Rank Order of Inherent Searching Responses of

 Cotesia congregata (Say) to Six Plants^{e,b}

^a Analysis was performed using SAS GLM (SAS Institute, 1985); data were transformed by sqrt (searching time + 0.5) prior to analysis to correct for normality of residuals.

^bResults of complete ANOVA are shown in Table I.

Table III. Results of Analysis of Variance Performed to Test the Effects of Strain (U.M. or WYE) and Plant Species (Cauliflower, Tobacco, and Tomato) on the Searching Responses of *Cotesia congregata* (Say) Exposed to Their Hornworm Hosts Only at Emergence to Each of the Three Plant Species^a

			وبودائي ويعون الثار ويهيز الثاني ويستعا
Source of variation	df	F value	Р
Parasitoid Strain	1	4.10	0.0465
Plant Assayed	2	10.09	0.0001
Parasitoid Strain			
× Plant Assayed	2	3.85	0.0257
Error	79		

"Analysis was performed using SAS GLM (SAS Institute, 1985); all assumptions for ANOVA were met.

tomato, none of the females tested (n = 34) chose to land on cauliflower (Fig. 3B).

Effects of Postemergence Experience with Tobacco or Parsley on Searching and Landing Responses of *C. congregata* to These Plants

Plant experience at emergence altered the searching responses of 3-day-old females of *C. congregata* to tobacco or parsley, as indicated by the significant (P = 0.0061) two-way interaction of postemergence exposure and plant assayed (Table IV). However, this significant interaction was due entirely to the effects of postemergence exposure to parsley. Females exposed only to their hosts at emergence searched longer on tobacco than they did on parsley (P = 0.0001), as did females exposed to tobacco and their hosts at emergence (P = 0.0001), but females exposed to parsley and their hosts searched as long on parsley as



Fig. 3. Searching and landing responses of females from two strains of *Cotesia congregata* (Say) to tobacco, cauliflower, and tomato. (A) No-choice assays of searching responses to these plants. Each bar represents the ls mean \pm SE response of 12–15 individuals. Means for each strain with different letters above the bars are significantly different (P < 0.02). (B) Landing preferences for these plants. No females from either the U.M. (n = 20) or the WYE (n = 14) strains chose to land on cauliflower and showed no preferences for tobacco or tomato (P = 0.704).

they did on tobacco (P = 0.3988), as shown in Fig. 4A. Females exposed to tobacco and their hosts searched as long on tobacco (P = 0.3214) or on parsley (P = 0.7216) as females exposed to their hosts only. However, when females were exposed to parsley and their hosts at emergence, they searched longer on parsley than females exposed only to their hosts (P = 0.0001). Postemergence experience with parsley did not affect searching time on tobacco (P = 0.1763).

Postemergence experience with tobacco and hosts or with parsley and hosts affected the landing preferences of 3-day-old females of *C. congregata* to tobacco and parsley similarly. As shown in Fig. 4B, females exposed only to their hosts

Source of variation	df	F value	Р
Postemergence Exposure	2	11.85	0.0001
Plant Assayed	1	37.75	0.0001
Postemergence Exposure			
× Plant Assayed	2	5.62	0.0061
Error	57		

 Table IV. Results of Analysis of Variance Performed to Test the Effects of Postemergence

 Exposure to a Moderately Attractive Host Plant (Tobacco) or to a Weakly Attractive

 Nonhost Plant (Parsley) on the Searching Response of Cotesia congregata (Say) to

 These Two Plant Species^a

^{*a*} Analysis was performed using SAS GLM (SAS Institute, 1985); data were transformed by sqrt (searching time + 0.5) prior to analysis to correct for normality of residuals.

at emergence showed no preference for tobacco or parsley (P = 0.08), but females exposed to their hosts and tobacco showed a strong preference for landing on tobacco rather than on parsley (P = 0.008), even though this same postemergence experience did not induce an increased searching response to tobacco (Fig. 4A). Interestingly, females exposed to their hosts and parsley at emergence also showed a preference for landing on tobacco rather than on parsley (P = 0.0204), even though this same postemergence experience induced an increased searching response to parsley (Figs. 4A and B).

DISCUSSION

Our results demonstrate that postemergence experience with one plant species in the presence of the caterpillar host can affect the searching or landing responses of reproductively mature females of *C. congregata* to the plant they experienced at adult emergence or to other, taxonomically unrelated plants. Our results also demonstrate that postemergence experience affects searching responses and landing preferences differently and that these effects may vary with respect to the plant experienced by emergent females and the plants offered for comparison in assays.

Cross-induction of orientation responses has been reported for a few saprophagous or phytophagous species (see Introduction) but has not been reported previously among insect parasitoids. Although the phenomenon of cross-induction may be coincidental, i.e., due to the underlying physiological mechanisms involved in learning or to the type of postemergence experience provided (Jaenike, 1983; Vet *et al.*, 1990), it may also have adaptive significance, particularly for herbivorous species that can utilize several plants or for entomophagous



Fig. 4. Effect of postemergence experience with the hornworm host and with tobacco or parsley on the searching and landing responses of *Cotesia congregata* (Say). (A) No-choice assay of searching responses to tobacco or parsley. Each bar represents the ls mean \pm SE response of 9 or 10 individuals. (B) Landing preferences for tobacco or parsley. Each bar represents the proportional responses of 21–30 individuals. See text for further explanation.

species, such as *C. congregata*, which can utilize herbivorous hosts occurring on many plant species.

For example, the listed hosts of *C. congregata* include 15 sphingids (10 genera) and one noctuid, *Trichoplusia ni* (Hubner) (Krombein *et al.*, 1979) in addition to at least three additional sphingids in two previously unlisted genera (Kester and Barbosa, 1991b). Most of these sphingid hosts utilize plant hosts occurring in only one or a few plant families but their cumulative host-plant range is quite broad, representing as many as 40 plant families in Maryland alone (Hodges, 1971; Tietz, 1972; Kester and Barbosa, 1991b). Many of these sphingid hosts occur sympatrically and some share similar phenologies but often

occur on different plants. The availability of different sphingids also varies over the growing season so that emergent females of *C. congregata* may have to locate new host species occurring on plants other than the one on which they underwent development. Given the distribution and abundance of hosts for most populations of *C. congregata*, postemergence induction of a single plant preference makes little sense, particularly if females were inhibited from dispersing to new habitats where appropriate hosts could be found.

The combined differential effects of postemergence experience with a novel plant on searching and landing preferences may be such that the range of plants considered by foraging females would be modified, at least in some cases, to include the experienced novel plant without excluding inherently attractive plants. For example, postemergence experience with the caterpillar host and parsley, a highly novel plant, induced an increased searching response to parsley but an increased landing preference for tobacco over parsley (Figs. 4A and B). In contrast, postemergence experience with the host and tobacco did not induce changes in searching responses to tobacco but did induce a landing preference for tobacco over parsley (Figs. 4A and B). Similar results are reported by Sheehan and Shelton (1989) for Diaeretiella rapae M'Intosh (Hymenoptera: Aphidiidae), although the type of postemergence experience provided in their work included oviposition and lasted several days (Sheehan and Shelton, 1989). For example, compared to females of D. rapae exposed to host and collard (a common host plant), females exposed to hosts and to potato (a novel host plant) search longer on potato but do not show increased orientation to potato in nochoice flight trials. In contrast, compared to the potato-experienced females, the collard-experienced females do not search longer on collard but show a trend for increased orientation to collard, compared to females exposed to hosts and potato (Sheehan and Shelton, 1989).

In part, differential effects of postemergence experience on searching and landing preferences may be due to the different type of stimuli that elicit landing and searching behavior in *C. congregata*. For example, inexperienced females from our U.M. or WYE strains of *C. congregata* searched at least as long on cabbage as they did on tobacco or tomato, but when offered all three plants in a flight chamber, none of the females tested chose to land on cabbage (Figs. 3A and B). Similar disparities in prealighting and postalighting preferences have been reported for butterflies (Rauscher *et al.*, 1981; Stanton, 1982; Papaj and Rauscher, 1983). The differential effects of postemergence experience on searching and landing responses may also reflect the type of postemergence exposure provided in our work, i.e., direct contact with artificially damaged leaves only, or may reflect the importance of visual stimuli in flight orientation and landing (Arthur, 1966, 1967; Wardle, 1990; Wardle and Borden, 1990). Newly emerged *C. congregata* occasionally hover around the plant on which their hosts are located and this hovering experience may be necessary for learning other olfac-

tory or visual cues used in flight orientation or landing. If the postemergence experience provided in our work had included hovering, subsequent flight responses may have been affected differently, but this remains to be tested.

The effects of postemergence experience on searching responses and landing preferences also varied with respect to the plant species experienced and the selection or choices of plant species offered in assays. For example, postemergence experience with the caterpillar host and one of six plant species affected the searching responses of 2-day-old females of C. congregata but effects varied with respect to the plant experienced (Figs. 2A-F). Similarly, postemergence experience with the host and tobacco, a relatively attractive plant, induced a landing preference for tobacco over parsley in 3-day-old females (Fig. 4B), even though it does not induce a landing preference for tobacco over tomato in females from both our U.M. and WYE strains of C. congregata (Kester and Barbosa, 1991b). Although we have considered only a few of the actual number of plant species that may be encountered by C. congregata under field conditions, our results suggest that postemergence learning, and associative learning in general, may be more complex than suggested by traditional two-way comparisons, particularly when separate components of foraging behavior are considered.

As a caveat, we note that our work has considered the response of *C.* congregata to plants in the absence of the host, host products, or host feeding damage and that reproductively mature females of other parasitoid species can learn to distinguish between the presence and the absence of these host-derived cues (Vet, 1983; Turlings *et al.*, 1990). Thus, the effects of postemergence experience on both landing preferences and searching responses may be modified by the presence of host-derived cues. However, we also note that *C. congregata* and other parasitoid species show strong responses to plants or plant-derived stimuli in the absence of host-derived cues, or perhaps at low host densities, plant-derived stimuli may be more important in determining landing and searching responses of insect parasitoids, especially for ovipositionally inexperienced females.

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