Behavioral and Ecological Constraints Imposed by Plants on Insect Parasitoids: Implications for Biological Control

K.M. KESTER* AND P. BARBOSA

Department of Entomology, University of Maryland, College Park, Maryland 20742

Interactions involving parasitoids, their herbivore hosts, and the plants on which their hosts are encountered are complex and dynamic. For example, parasitoids use plant stimuli for locating their hosts, but their survival may be adversely affected by plant allelochemicals ingested by their hosts. Generalizing from our investigations involving *Cotesia congregata* (Say) (Hymenoptera: Braconidae), we suggest that under some conditions, populations of insect parasitoids may adapt to specific plants or to the allelochemicals produced by these plants. Adaptations to plants in insect parasitoids can include increased survivorship and fixation of some components of foraging behavior and may be facilitated by postemergence learning. Variation in the ability to tolerate plant allelochemicals among parasitoid populations may be exploited to enhance biological control efforts. © 1991 Academic Press, Inc.

KEY WORDS: Tritrophic level interactions; population differences; plant allelochemicals; local adaptation; biological control; *Cotesia congregata* (Say), Braconidae; *Manduca sexta* L., Sphingidae.

Introduction: Parasitoids, Herbivores, Plants, and Plant Allelochemicals

Interactions involving parasitoids, their herbivore hosts, and the plants on which their hosts are encountered are complex and dynamic. For example, some parasitoids are attracted to plant extracts or to volatiles from the food plants of their hosts (Thorpe and Candle, 1938; Monteith, 1955, 1958; Arthur, 1962; Herrebout and van der Veer, 1969; Nettles, 1979, 1980; Altieri *et al.,* 1981; Nordlund *et al.,* 1988; Ding *et al.,* 1989a). In a few cases, specific chemical attractants of host food plants have been identified (Read *et al.,* 1970; Elzen *et al.,* 1983,

1984a; Lecomte and Thibout, 1984; Williams *et al.,* 1988). Additionally, there is strong evidence that parasitoids can detect the presence of plant chemicals in the frass of their hosts and differentiate between the diets or plants consumed by their hosts (Sauls *et al.,* 1979; Thompson *et al.,* 1983; Mohyuddin *et al.,* 1981; Roth *et al.,* 1978; Nordlund and Sauls, 1981; Elzen *et al.,* 1984b). Differential responses to plant-derived stimuli may explain why parasitism of hosts occurs on some plants but not on others or at different levels on different plants (Walker, 1940; Zwolfer and Kraus, 1957; Salt, 1958; Sekhar, 1960; Arthur, 1962; Haynes and Butcher, 1962; Bombosch, 1966; Streams *et al.,* 1968; Young and Price, 1975; Martin *et al.,* 1976; Harrington and Barbosa, 1978; Zehnder and Trumbule, 1984).

As indicated by the studies cited above, parasitoids use plant-derived stimuli as cues in both host habitat and host location (Vinson, 1975, 1976, 1981, 1984). However, parasitoid responses to habitat odors or to other olfactory stimuli can vary with their physiological state (Thorpe and Candle, 1938; Nishida, 1956; Herrebout and van der Veer, 1969; Shahjahan, 1974; Hérard *et al.,* 1988a; Lewis and Takasu, 1990). Also, variation in parasitoid responses to habitat stimuli may reflect genotypically fixed variation within (Prevost and Lewis, 1990) or among populations (Bouletreau and David, 1981; Kester and Barbosa, 1991). Parasitoid responses to plants can also be modified through experience. For example, exposure to habitat cues during larval development, i.e., preimaginal conditioning, may affect orientation responses of parasitoids to plants (Thorpe and Jones, 1937; Vinson *et al.,* 1977; Vet, 1983; Luck and Uygun, 1986). Similarly, exposure to plant-based stimuli at or immediately following adult emergence can affect subsequent orientation, searching, or ovipositional responses of parasitoids to plants or host habitats (Vet, 1983; Wardle and Borden, 1985; Hérard *et al.,* 1988b; Kester and Barbosa, 1991). Orientation responses can be dramatically modified when adult parasitoids are exposed to habitat stimuli in association with their host or its products, especially when oviposition occurs (Monteith, 1963; Arthur, 1966, 1971; Taylor, 1974; Vinson

---

* Current address: Department of Biology, University of California, Santa Cruz, California 95064.

et al., 1977; Sandlan, 1980; Vet, 1983; Vet and van Op-zeeland, 1984, 1985; Dmoch *et al.,* 1985; Drost *et al.,* 1986, 1988; Lewis and Tumlinson, 1988; Ding *et al.,* 1989b; Sheehan and Shelton, 1989; Kaiser *et al.,* 1989; Wardle and Borden, 1989; Turlings *et al.,* 1989; Kaas *et al.,* 1990; Vet *et al.,* 1990). Finally, parasitoid responses to plants may reflect broader foraging strategies resulting from past selective pressures (van Alphen and Vet, 1986; Lewis *et al.,* 1990).

In addition to their role in host location, plants can affect the suitability of hosts for insect parasitoids. For example, parasitoid fitness is often affected by the plant species or cultivar on which the host feeds (Flanders, 1942; Narrayanan and Subba Rao, 1955; Smith, 1957; Pimentel, 1966; Cheng, 1970; Zhody, 1976; Blumberg and DeBach, 1979; and see Bergman and Tingey, 1979; Price *et al.,* 1980; Boethel and Eickenbary, 1986). In several cases, plant effects on parasitoid fitness have been related to the presence or concentration of plant allelochemicals (Narayanan and Subba Rao, 1955; Smith, 1957; Altahtawy *et al.,* 1976; Smith, 1978; Thorpe and Barbosa, 1986). Plant allelochemicals ingested by herbivores can be transferred to the next trophic level and have been recovered from several parasitoids (Jones *et al.,* 1962; Reichstein *et al.,* 1968; Rothschild *et al.,* 1977; Smith, 1978; Benn *et al.,* 1979; Campbell and Duffey, 1979; Barbosa and Saunders, 1985; Barbosa *et al.,* 1986). Although adverse effects of plant allelochemicals on insect parasitoids may be indirect, i.e., due to a reduction in herbivore host quality, direct effects have been demonstrated in a few cases (see below).

Since plants may benefit from the action of natural enemies on herbivores, Price *et al.* (1980) suggested that the plant defense theory should consider the third trophic level as a component of plant defense against herbivores. However, experimental studies involving tritrophic level interactions have yielded somewhat conflicting results. For example, parasitoids orient to volatiles released by damaged plants (Whitman and Eller, 1990) and can learn to orient to plant volatiles induced by host feeding (Turlings *et al.,* 1991). However, parasitoid survival can also be adversely affected by plant allelochemicals ingested by their hosts and in some cases, these allelochemicals are induced by herbivore feeding. For example, leaf damage induces increased levels of nicotine and nornicotine in tobacco plants (Baldwin, 1988), yet nicotine adversely affects the performance and survival of several parasitoid species (Barbosa *et al.,* 1986; Gunasena *et al.,* 1990).

Perhaps plants can "deceive" parasitoids for their immediate benefit. However, if parasitoids are attracted to specific plants that decrease the survival of their progeny, they will be of little benefit to these plants over time. Parasitoids faced with this paradox would suffer extinction unless they adapted to utilize new hosts or to increase their survival on these plants. Behaviorally,

parasitoids might increase their ability to detect or respond negatively to plant allelochemicals that adversely affect the survival of their offspring and avoid oviposition in hosts that have ingested these plant allelochemicals. Physiologically, parasitoids might develop an increased ability to tolerate these plant allelochemicals during larval development. In addition to being theoretically interesting, investigations of parasitoid adaptations to plant allelochemicals may have useful implications for biological control.

In this paper, we discuss our work with two populations of *Cotesia congregata* (Say) (Hymenoptera: Braconidae), a larval endoparasitoid of *Manduca sexta* L. (Lepidoptera: Sphingidae), which differ both in their degree of exposure to tobacco *(Nicotiana tobacum* L.) and in their behavioral and physiological responses to nicotine. We then suggest that such population differences in insect parasitoids may be facilitated by postemergence learning, as previously hypothesized for phytophagous insects (Jaenike, 1983, 1988; Smith, 1987; Papaj and Prokopy, 1988). Next, we suggest that behavioral and physiological responses of insect parasitoids to plant allelochemicals may provide an adaptive match to temporal and spatial patterns of herbivore abundance. Finally, we discuss the implications of our work for biological control in agro-ecosystems. Although plant effects on parasitoid-host interactions may also include those due to physical attributes, our work has focused on chemical features.

C. congregata, M. sexta, and Nicotine

Both *C. congregata* and *M. sexta* are native to the Americas. The host range of *C. congregata* is largely restricted to the Sphingidae (Krombein *et al.,* 1979) and the host plant ranges of its specific herbivore hosts are often restricted to one or a few plant families (Hodges, 1971; Tietz, 1972). However, there is considerable diversity in the plants to which *C. congregata* may be exposed when the plant hosts of its sphingid hosts are considered collectively. For example, sphingid hosts restricted to plant families such as Vitaceae, Bignoniaceae, or Pinaceae may occur sympatrically with those restricted to Solanaceae. The ability of *C. congregata* to locate and utilize hosts on such different plants suggests that this parasitoid has been able to respond and adapt to an array of plant chemicals. If available hosts are usually encountered on one noxious plant species over time, this adaptability could lead to the formation of populations of *C. congregata* locally adapted to this plant species and its allelochemicals, just as herbivore populations can become locally adapted to abundant food plants (Fox and Morrow, 1981).

The effects of tobacco and its major alkaloid, nicotine, on interactions involving *C. congregata* and *M. sexta* have been well-studied. Observed lower rates of

parasitism for *M. Sexta* feeding on tobacco than on other solanaceous plants were first suggested to be due to the influence of nicotine on the behavior of C. *congregata* by Morgan (1910) and later by Gilmore (1938a,b). Thurston and Fox (1972) suggested a similar mechanism to account for the differential rates of parasitism of *M. sexta* feeding on flue and burley tobacco varieties and demonstrated that a single application of nicotine on the cuticle of *M. sexta* inhibited larval emergence of *C. congregata.* Although most (98–99%) ingested nicotine is excreted by *M. sexta,* some is absorbed into the hemolymph (Self *et al.,* 1964) and has been recovered from cocoon silk, meconium, and adults of *C. congregutu* (Barbosa *et al.,* 1986). Performance and survival of C. *congregata* are reduced when *M. sexta* feeds on tobacco plants with a high rather than low nicotine concentration (Thorpe and Barbosa, 1986) or on a laboratory diet with nicotine rather than on a nicotine-free diet (Parr and Thurston, 1972; Barbosa *et al.,* 1986, 1991). Also, performance and survival responses of *C. congregata* to nicotine in the host diet are dosage dependent and similar to those found for *M. sexta,* except that *C. congregata* shows greater sensitivity to nicotine than does *M. sexta* (Barbosa *et al.,* 1991). Since ECD and ECI indices for *M. sexta* are not affected by ingestion of 0.1% nicotine, adverse effects on performance and survival are attributed to the direct action of nicotine on *C. congreguta* (Bentz and Barbosa, 1990; but see Baldwin, 1988).

The cumulative results of these studies apparently contradict the predicted role of third-trophic-level organisms in the evolution of plant defense, in that nicotine deleteriously affects the performance and survival of both *C. congregata* and its host, *M. sexta.* To our knowledge, this system is the only one for which a plant allelochemical has been demonstrated to directly affect the survival of an insect parasitoid and for which the same plant allelochemical has been suggested to also affect the behavior of an insect parasitoid. Thus, it provides an excellent model system for investigating the ability of an insect parasitoid to behaviorally and physiologically adapt to a plant allelochemical.

Population and Strain Differences in Host Habitat Responses of Insect Parasitoids

Population or strain differences in the behavioral or physiological responses of insect parasitoids to different host habitats have been considered in only a few studies. For example, adults of *Asobara tabida* Nees (Hymenoptera: Braconidae), a larval endoparasitoid of fungivorous *Drosophila* spp. (Diptera: Drosophilidae), orient to host habitat odors. Adults originating from two different microhabitats (fermenting fruits or decaying plants) prefer the odor of the microhabitat from which they originate (Vet *et* al., 1984). Since females will mate willingly only with males from their own strain, these strains are now considered to be sibling species, *Asobara tabida* and *A. rufescens* Foerster, which are reproductively isolated by their different microhabitat preferences. Survival of each species is higher when they develop in the major host of the preferred microhabitat than when they develop in the major host of the nonpreferred microhabitat (Vet and Janse, 1984).

Geographic variation in ethanol tolerance among parasitoids parallels that of their drosophilid hosts (Carton *et al.,* 1986). *Drosophila* spp. utilize fermenting substrates and have adapted to the high concentrations of ethanol present in their habitats by detoxifying ingested ethanol. Likewise, hymenopterous parasitoids of wine-cellar-dwelling drosopholids such as *A. tabida, Leptopilina boulardi* (Barbotin *et al.*) (Eucoilidae), and *Ganaspis* spp. (Eucoilidae) show a greater tolerance to ethanol than those collected from habitats with lower concentrations of ethanol (Bouletreau and David, 1981). Since ethanol tolerance is limited to females, it is presumed to be a consequence of selection affecting only the sex which seeks out hosts in fermenting habitats.

Do Populations of C. congregata Differ in Their Responses to Nicotine?

Our research has addressed several related questions: (1) Do populations of an insect parasitoid differ in their ability to utilize hosts feeding on different plants or hosts fed on diets with specific plant allelochemicals? (2) Do populations of an insect parasitoid differ in their behavioral responses to plants on which they typically or atypically encounter their primary host? (3) Can an insect parasitoid detect the presence of a plant allelochemical that deleteriously affects its survival and if so, do populations differ in their response to this plant allelochemical? (4) How does learning mediate population differences in behavioral or physiological responses to plants or to plant allelochemicals?

The populations of *C. congregata* used in our investigations originated from two study sites selected on the basis of their location, history, and present abundance of tobacco. The "U.M." site (Tobacco Research Farm, Upper Marlboro, Prince George's County, MD; 38" 52' latitude) is located in an area in which tobacco has been intensely cultivated for over 350 years. The "WYE" site (Wye Research and Education Center, Wye, Queen Anne's County, MD; 38" 55' latitude) is located 56 km away and on the other side of the Chesapeake Bay in an agriculturally diverse area where tobacco has been rarely cultivated for ca. 250 years. At both sites, the most abundant host species are *M. sexta* and *Manduca quinquemaculata* (Haworth) and thus, most available hosts will be encountered on solanaceous plants. However, at U.M., these hosts typically occur on tobacco, whereas at WYE, these hosts occur on tomato, a plant

TABLE 1

Night-Flying Sphingids Captured by Black-Light Trapping at U.M. and WYE in 1988

Species[a]	Proportion of all moths captured at	
	U.M.[b]	W Y E
Manduca *sexta*[d]	0.49	0.16
Manduca *quinquemaculata*[d]	*0.24*	*0.33*
Hyles lineata	0.11	*0.03*
Ceratomia undulosa	0.04	0.04
Darapsa *myron*[d]	*0.03*	*0.04*
Paratrea *plebja*[d]	*0.03*	0.11
Paonis *myops*[e]	*0.02*	0.18
Darapsa *pholus*	0.01	0
Paonis *excaecatus*[e]	0.01	0.01
Eumorpha *pandorus*[d]	<0.01	*0.02*
Eumorpha *achemon*[d]	<0.01	0
Ceratomia *catalpae*[d]	co.01	0
Smerinthus *jamaicensis*[a]	<0.01	0
Sphecodina *abbottii*[d]	<0.01	0
Xylophanes *tersa*	to.01	0
Cressonia *juglandis*	*0*	0.02
Pachysphinx *modesta*	*0*	0.02
Agrius *cingulatus*	0	<0.01

[a] Identification based on Hodges (1971).

[b] 384 moths captured, 5/16–9/6/88.

[c] 262 moths captured, 5/13–9/18/88; abundance of *M. sexta* and *M. quinquemaculata* may be underrepresented (trap contents destroyed by beetles on 3 nights during peak flight activity).

[d] Recorded hosts of *Cotesia congregata* (= *Apanteles congregatus*) (Krombein *et al.*, 1979).

[e] Additional hosts of C. *congregata* (K. M. Kester, unpublished).

TABLE 2

Major Plant Family Associations of Night-Flying Sphingids Captured at U.M. and WYE in 1988

Plant family[a]	Proportion of sphingid population at	
	U.M	WYE
Solanaceae	0.73[b] (2)[c]	0.51 (2)[d]
Vitaceae	0.05 (5)	0.07 (3)
Oleaceae	0.04 (1)	0.04 (1)
Bignoniaceae	0.03 (2)	0.11 (1)
Rosaceae	0.02 (1)	0.18 (1)
Salicaeae	0.01 (2)	0.01 (1)
All others	0.11 (1)'	0.06 (3)'

[a] Plant family associations based on recorded food plants for species restricted to a single plant family and/or on larval recoveries of species recorded on more than one plant family (Hodges, 1971; Tietz, 1972; Gleason and Cronquist, 1963; Kester, unpublished). See Table 1.

[b] Proportion of all individual sphingids captured.

[c] Numbers in parentheses show number of host species associated with each plant family.

[d] Proportion may be underrepresented (see comments for *Manduca* spp. in Table 1).

[e] Includes *Hyles lineata*, a broad generalist with recorded food plants in 18 families.

[f] Includes Juglandaceae, Convolvulaceae, and other plant families listed for *H. lineata*.

that does not contain nicotine. Relative abundance of the available host species at the two sites was fairly stable over the 4 years. Potential sphingid hosts and their relative abundance at each site are listed in Table 1. Common food plants of these herbivores, by family, are shown in Table 2. At both sites, *M. sexta* and *M. quinquemaculata* had similar phenologies, and their relative abundance over the growing season, compared to all other hosts, is shown in Fig. 1.

Populations differ in their survivorship responses to nicotine. Parasitoids collected from *M. sexta* on tobacco at U.M. and from *M. sexta* on tomato at WYE differed in their survivorship responses to the concentration of nicotine in their hosts' diet (Fig. 2). Larval, pupal, and adult survivorship of parasitoids from both populations was higher when their hosts fed on tomato plants rather than on tobacco plants. However, when the progeny of these parasitoids developed in hosts fed on a 0.3% nicotine diet or on the same diet without nicotine, **parasitoids from U.M. exhibited increased larval and pupal survivorship after one generation of exposure to nicotine. In contrast, those from** WYE **showed decreased survivorship and did not survive beyond two** genera-

tions of exposure to dietary nicotine. Overall, the U.M. strain of *Cotesia congregata* showed greater tolerance to nicotine than the WYE strain (Kester and Barbosa, **submitted).**

Populations differ in their ovipositional preferences in the field. The U.M. and WYE populations of *Cotesia congregata* differed in their field ovipositional preferences for *M. sexta* on tobacco or tomato early in the **growing season, when both host and parasitoid popula**tions were relatively small. *Cotesia congregata* at WYE preferred to oviposit in hosts on tomato rather than in hosts on tobacco when equal densities of third-instar *M. sexta* were presented for 2 days, whereas *Cotesia congregata* at U.M. showed no preference (Table 3A). Since
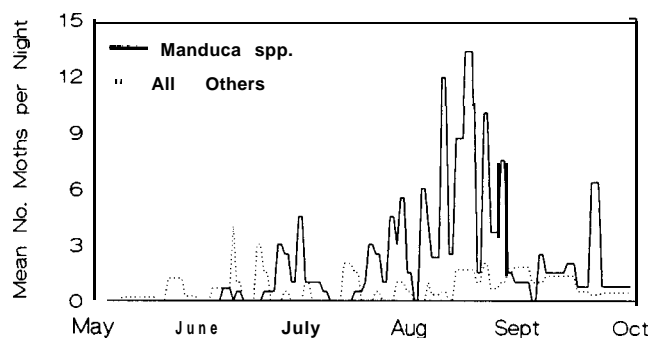

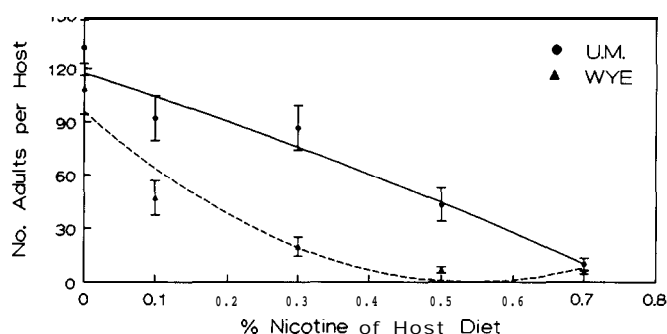FIG. 1. Black light captures of sphingids at U.M. in 1988.

FIG. 2. Adult survivorship responses of two populations of *Cotesia congregata* (Say) to host, *Manduca* sexta L., fed on diets with selected concentrations of nicotine. Responses of the two populations differ ($P = 0.0001$, $r^2 = 6720,115$ *df*). Response of the U.M. population (triangular markers and unbroken line) is best described by: sqrt (No. adults per host) $= 10.54 - 2.47$ [nicotine] $- 14.0$[nicotine]^2 ($P = 0.0001$, $r^2 = 0.5246$, 65 *df*). Response of the WYE population is best described by: sqrt (No. adults per host) $= 9.75$ 26.85[nicotine] $+ 19.75$[nicotine]^2 ($P = 0.0001$, $r^2 = 0.7089$, 50 *df*). Markers and regression lines are based on back-transformed least-squares means $\pm$ SE. (From Kester and Barbosa, 1991.)

parasitoids present at this time were most likely those which had overwintered in proximity to our study plots and had limited, if any, ovipositional experience, inherent preferences were most likely to be detected at this time.

However, both populations of **Cotesia congregata** showed no preferences for **M. sexta** on tobacco or tomato later in the season, when host populations were large (Table 3B). Seasonal fluctuations in ovipositional responses within these populations may have been due to a combination of factors, including experiential effects or responses to increasing host density and/or host feeding damage over the season. In addition, there may have been an influx of parasitoids from neighboring al-

TABLE 3

Field Ovipositional Preferences of Two Populations of *Cotesia congregata* (Say) for **Manduca sexta** L. on Tobacco or Tomato",*

	Percentage oviposition on		
Population	Tobacco	Tomato	
A. Early season			
U.M. (7/16–18/87)	12.9 ± 4.4	7.7 ± 5.0	**P > 0.05**
WYE (7/18–20/87)	18.5 ± 4.4	44.0 ± 4.4	**P = 0.0075**
B. Late season			
U.M. (8/2–4/87)	54.8 ± 5.2	57.4 ± 5.2	**P > 0.05**
WYE (8/1–3/87)	22.2 ± 5.2	22.3 ± 5.3	**P > 0.05**

[a] Analyses performed using SAS GLM (SAS Institute, 1985); $n = 16$ patches each of tomato and tobacco at each site.
[b] From Kester and Barbosa (1991).

TABLE 4

Searching Responses of Females from Two Strains of *Cotesia congregata* (Say) to Tobacco and Tomato (Least-Squares Means $\pm$ Standard Error)[a,b]

	Mean time spent searching on		
Strain	Tobacco	Tomato	
U.M.	50.9 ± 4.4	36.1 ± 4.4	**P = 0.0108**
WYE	24.6 ± 4.2	40.3 ± 4.1	**P = 0.0087**
	P = 0.0001	**P =** 0.4710	

[a] Analyses performed using SAS GLM (SAS Institute, 1985). Data were transformed by sqrt (time + 0.5) prior to analysis to correct for normality of residuals; $n = 35$-36 for each strain on each plant.
*From Kester and Barbosa (1991).

ternate hosts late in the season ("local immigration"). Local immigration of "nonadapted" **Cotesia congregata** into tobacco plots at U.M. could also explain why survivorship of U.M. and WYE parasitoids (recovered in late August) was similar when they developed in **M. sexta** fed on tobacco plants but different over two generations of exposure to dietary nicotine (see preceding section) (Kester and Barbosa, 1991).

Strains differ in their behavioral responses to plants. In a series of laboratory studies, we compared selected behavioral responses of females from the same two populations of **Cotesia congregata.** The U.M. strain originated from **M. sexta** on tobacco and the WYE strain originated from **M. sexta** on tomato. Both strains were reared in **M. sexta** fed on a semisynthetic laboratory diet. Parasitoids were permitted contact with their hosts for the first 3-5 h following emergence but had no exposure to any plant stimuli prior to being tested 2-3 days later.

Although females from the two strains showed similar landing responses to artificially damaged tobacco and tomato plants, they differed in their searching responses to these plants. In choice landing assays conducted in a flight chamber, 67% of U.M. females ($P > 0.5$, **n** = 22) and 64% of WYE females **(P > 0.5, n** = 14) chose to land on tomato rather than on tobacco. However, when individual females were offered a disk of tomato or tobacco leaf in no-choice trials, WYE females searched longer on tomato and U.M. females searched longer on tobacco, as shown in Table 4. The two strains differed in their searching responses to other plants as well (Kester and Barbosa, 1991).

Strains differ in their searching responses to nicotine. To determine if **Cotesia congregata** can detect nicotine and if strain differences in searching responses to tobacco were related to differences in their response to nicotine, we assayed the searching responses of individual females from each strain to nicotine solutions of selected concentrations applied to the surface of a disk
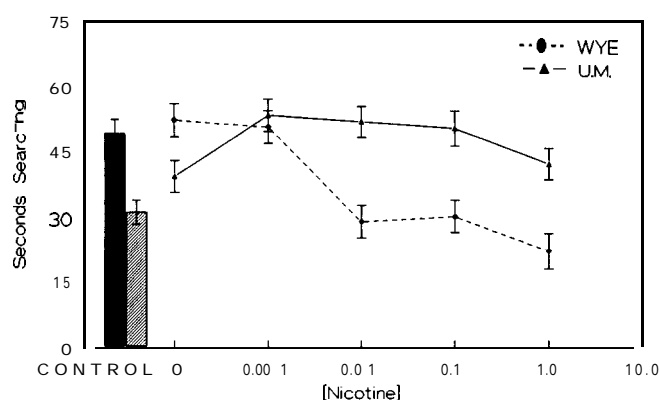
FIG. 3. Searching responses of females from two strains of *Cotesia* congregata (Say) to selected concentrations of nicotine applied to disks of tobacco leaf. Bars represent untreated tobacco control; 0% nicotine = acetone only (U.M. strain, slashed bar, triangular markers, and unbroken line; WYE strain, solid bar, circular markers, and broken line). Each bar or point represents the (least-squares mean ± standard error) response of 22-25 females. (From Kester and Barbosa, 1991.)

of tobacco leaf. Although females from both strains apparently detected the nicotine, their responses differed over the range of nicotine concentrations tested (Fig. 3). Overall, WYE females searched longer on disks treated only with the solvent (acetone) than on disks treated with nicotine, but searched for decreasing amounts of time in response to increasing nicotine concentration. In contrast, U.M. females searched less time on disks treated only with acetone than on nicotine-treated disks, but searched for similar amounts of time over the range of nicotine concentrations tested (Kester and Barbosa, 1991).

Postemergence Learning: Mechanism for Facilitating Local Adaptations to Plants?

Our results demonstrate that the two populations of *Cotesia congregata* differed in both their physiological and behavioral responses to nicotine. The U.M. parasitoids, originating from an area of intense tobacco cultivation, showed a greater tolerance to nicotine in their hosts' diet and more positive responses to direct contact with tobacco or with nicotine than the WYE parasitoids which originated from a more diverse agricultural area. Given the history of the U.M. population and the consistency of our results, local adaptation to nicotine in this population is strongly suggested.

However, given the probable yearly influx of non-adapted individuals within the U.M. population of *Cotesia congregata* and the phenotypic plasticity of behavioral responses to habitat stimuli in this species, as well as in other microgastrines, e.g., *C. marginiuentris* (Cresson) (Turlings *et al.,* 1989) and *Microplitis croceipes* (Cresson) (Drost *et al.,* 1986, 1988), how might adapta-

tions to nicotine evolve or be maintained? To address this question, we conducted a series of experiments based on field and laboratory observations of newly emerged adults of *Cotesia congregata* in which we determined how postemergence experience with plants affected the subsequent behavioral responses of *Cotesia congregata* to plants. All parasitoids used in these experiments developed in *M. sexta* fed on a semisynthetic (wheat germ) laboratory diet and had no exposure to plants other than that provided experimentally.

Behavior of newly emerged adults. Immediately upon emergence from their cocoons, females of *Cotesia congregata* walk to the upper surface of the leaf on which their host, *M. sexta,* is suspended, and they walk for several minutes while continuously palpating the leaf surface. Males generally emerge before females and aggregate on the upper leaf surface, where they engage in courtship displays and initiate mating. Both sexes occasionally hover around the plant and then return to upper leaf surfaces, where they resume examination, courtship, and mating behaviors.

Postemergence learning requires exposure during sensitive period. Exposing newly emerged females of *Cotesia congregata* to wild cherry, an inherently unattractive plant, and to their hosts O-4 h after emergence induced a positive searching response to wild cherry and an inhibited searching response to cabbage, an inherently attractive plant. However, inherent responses were not affected when females were exposed to their hosts O-12 h after emergence and to wild cherry 8-12 h after emergence. These results demonstrate that postemergence learning in *Cotesia congregata* required plant exposure in the presence of their host during a sensitive period immediately following emergence (Fig. 4). The induced
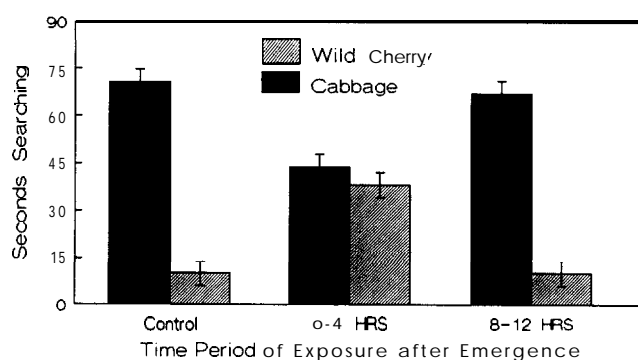

FIG. 4. Effect of timing of postemergence exposure to an inherently unattractive plant (cherry) on searching responses of *Cotesia congregata* (Say). Females in the control group were exposed only to their hosts O-4 h after adult emergence. Females in the 0- to 4-h group were exposed to both hosts and cherry leaves for O-4 h after adult emergence. Females in the 8- to 12-h group were exposed to hosts for O-12 h and to cherry leaves 8-12 h after adult emergence. Each bar represents the (least-squares mean ± standard error) response of 21 individuals assayed 48 h after emergence. (From Kester and Barbosa, 1991.)
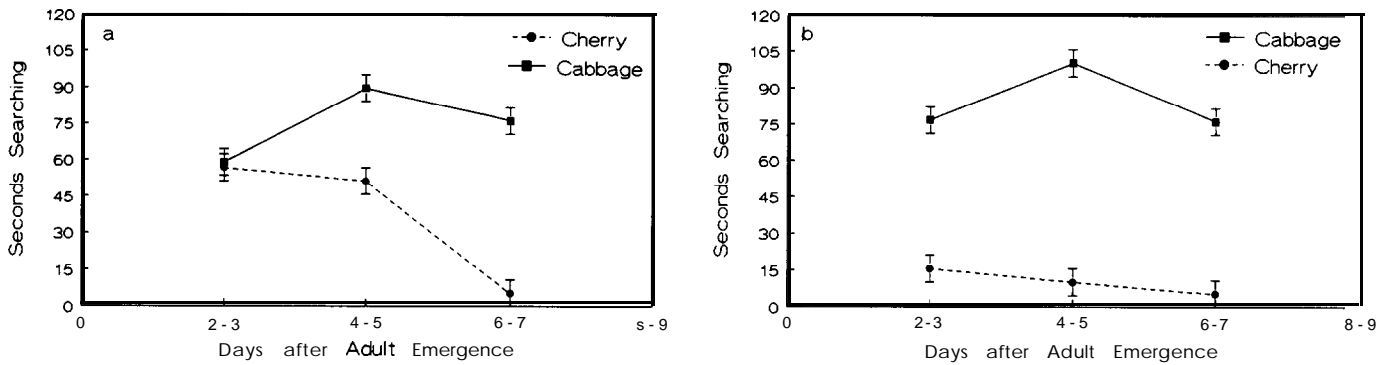
FIG. 5. Searching responses of Cotesia congregata (Say) to an inherently attractive (cabbage) or unattractive (cherry) plant. (a) Females exposed to cherry leaves and hosts O-4 h after adult emergence. (b) Females exposed only to their hosts O-4 h after adult emergence. Each point represents the (least-squares mean ± standard error. back-transformed from sqrt(seconds searching + 0.5)) response of 10 individuals. (From Kester and Barbosa, 1991.)

response to cherry was constant until it abruptly declined at 6-7 days after emergence, whereas the inhibited response to cabbage was released at 4-5 days after emergence (Fig. 5a). Searching responses to cabbage or wild cherry were not affected by exposure to hosts only (Fig. 5b) (Kester and Barbosa, 1991).

Cross-induction of searching responses through postemergence exposure to plants. Exposing newly emerged females of Cotesia congregata to plants in the presence of their hosts affects subsequent searching responses in several ways. As noted above, exposure to an inherently unattractive plant can induce a positive searching response to this plant and inhibit the searching response to an inherently attractive plant. However, exposure to some moderately attractive plants can also induce a positive searching response to other similarly attractive plants and inhibit searching responses to

FIG. 6. Effect of postemergence experience with cherry on the searching responses of Cotesia *congregata* (Say) to six plants. Females were exposed to their hosts and to cherry leaves O-4 h after adult emergence and were assayed at 48 h after emergence. Postemergence exposure to cherry significantly ($P < 0.0001$) modified the inherent rank order of searching responses. Stars denote a significant (P < 0.05) difference in the mean searching response of treatment females compared to that of control females (exposed only to their hosts O-4 h after adult emergence). Each bar represents the (least-squares mean ± standard error) response of 15-20 individuals. (From Kester and Barbosa, 1991.)

more attractive plants, thus disrupting the rank order of inherent responses (Fig. 6) (Kester and Barbosa, 1991). Although cross-induction of orientation responses has been reported for a few saprophagous or phytophagous species (Jaenike, 1983, 1988; Papaj and Prokopy, 1986), it has not previously been considered for insect parasitoids.

Effects of postemergence experience on landing responses. The effects of postemergence experience on landing responses of Cotesia congregata vary with respect to the plant experienced and the plants presented in flight assays. For example, landing responses of both U.M. and WYE females to tobacco or tomato, as noted in the preceding section, were not affected by postemergence experience with tobacco and hosts; 32% of the U.M. females tested ($P > 0.5$, $n = 22$) and 50% of the WYE females tested ($P > 0.5$, $n = 12$) chose to land on tobacco rather than on tomato. However, when U.M. females were offered a choice of tobacco or parsley in a flight chamber, postemergence experience with tobacco and hosts increased the likelihood that females landed on tobacco rather than on parsley, although searching responses were not affected (Figs. 7a and 7b). Interestingly, postemergence experience with parsley also increased the likelihood that U.M. females landed on tobacco rather than on parsley, even though it also induced an increased searching response to parsley (Figs. 7a and 7b).

Parasitoid foraging behavior is generally regarded as a complex and catenary process involving different stimuli at each step (Vinson, 1975, 1976; 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). Thus, postemergence experience with a particular plant may affect only some components of this process, e.g., searching time, and these effects may be overridden by later ovipositional experiences. Alternatively, differential effects of postemergence exposure to
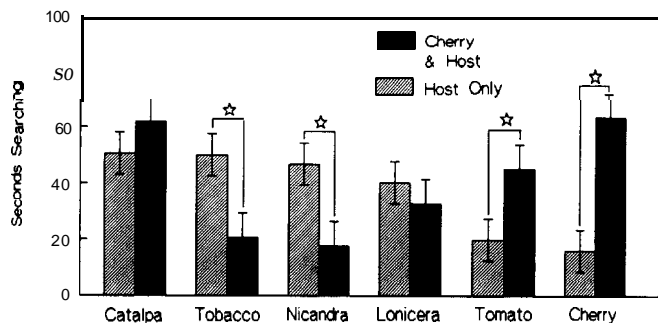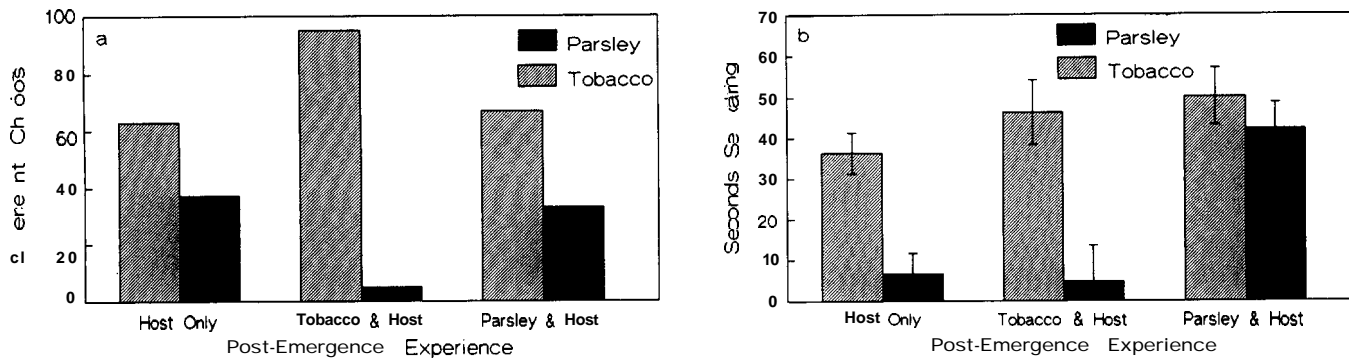
FIG. '7. Effects of postemergence experience with a common (tobacco) or novel (parsley) plant on the behavioral responses of *Cotesia congregata* (Say) to these plants. Females were exposed to leaves and/or hosts O-4 h after adult emergence and were assayed at 48 h after emergence. (a) Effects on landing preferences for whole plants. Compared to control females, more tobacco-experienced females *(P = 0.008)* and more parsley-experienced females *(P = 0.0204)* chose to land on tobacco than on parsley (generalized Fisher's exact test; Mehta and Patel, 1983). Each bar represents the choices of 21-30 individual females. (b) Effects on searching responses to leaf disks. Compared to control females (exposed to hosts only), females with experience with parsley significantly *(P = 0.0001)* increased their searching time on parsley (SAS GLM, SAS Institute, 1985). Each bar represents the (least-squares mean ± standard error) response of 10 individuals. (From Kester and Barbosa, 1991.)

plants on landing and searching responses may be due to the type of postemergence experience provided in our work, i.e., direct contact with artificially damaged leaves within a closed container. Newly emerged *Cortesia congregata* occasionally hover around the plant on which their hosts are located and this behavior may be necessary for learning other olfactory or visual cues used in flight orientation or landing. In any case, the results of our work support the hypothesis that landing and searching responses to plants involve at least some different stimuli.

Functions of postemergence learning in insects. By inducing habitat preferences, postemergence learning ("early adult experience") has been hypothesized to increase the likelihood of assortative mating, enhance potential linkage of adult behavioral preferences and progeny survival, and, thus, lead to genetic subdivisions within heterogeneous populations (Bush, 1969; Jaenike, 1983, 1988; Papaj and Prokopy, 1988). Alternatively, the "chemical legacy" hypothesis suggests that early experience may serve as a mechanism for the development of new, nongenetically determined habitat associations within insect populations (Corbet, 1985).

We suggest that the primary function of postemergence learning in *Cortesia congregata,* and perhaps other similar species, is to retain newly emerged adults for mating on the same plants on which they underwent development. This would encourage assortative mating, particularly among siblings, and thus could facilitate local adaptations for increased progeny survival on specific plants, under conditions of sufficient selective pressure. Similarly, postemergence experience may also facilitate behavioral adaptations. By modifying inherent searching responses of females to plants, postemergence experience affects foraging behavior both directly

and indirectly. For example, postemergence experience increases the time that females will spend searching on some plants and decreases the time they will spend searching on others. Postemergence experience with a specific plant may also increase the likelihood that first ovipositional experiences will occur with hosts in the original habitat.

However, since searching and flight responses of *Cortesia congregata* to specific plants are not directly related, it is possible that postemergence experience can facilitate the genetic fixation of some behaviors, while maintaining the phenotypic plasticity of others. For example, behavioral responses to plant stimuli may be modified through experience but the ability to detect or respond to plant-derived stimuli may be heritable (Prevost and Lewis, 1990). Also, parasitoid responses to plants or host habitats can differ between the sexes (McAuslane et al., 1990), perhaps reflecting differential selective pressures for mate or habitat location (Bouletreau and David, 1981). Since both males and females of *Cortesia congregatu* aggregate on plants immediately after adult emergence and those which remain within this habitat are more likely to mate than those which disperse, increased responsiveness to short-range olfactory and chemotactile plant stimuli, as well as increased responses to specific plant allelochemicals, may thus be facilitated as a consequence of postemergence learning.

Implications for Biological Control Theory and Practice

To understand how plants or plant allelochemicals affect parasitoid-host interactions, we must first understand how plants or plant allelochemicals affect the behavior and survival of insect parasitoids. However, how a specific plant affects the behavior or survival of a

KESTER AND BARBOSA

parasitoid may be determined, in part, by the degree of association between the parasitoid and its herbivorous host, as well as the relative abundance of this host and the plant species on which it is encountered over time. If so, parasitoid populations which differ with respect to the relative abundance of hosts on a particular plant species may also differ in their responses to this plant or the allelochemicals it contains.

The two populations of **Cortesia congregata** compared in our work were similar in that the most abundant hosts for both were **Manduca** spp. feeding on solanaceous plants. However, for over 350 years, these hosts have been encountered by the U.M. population on a noxious plant, tobacco, which contains nicotine, an allelochemical that adversely effects the survival of **Cortesia congregata,** whereas the same hosts are usually encountered by the WYE population on tomato, which does not contain nicotine. As described earlier, these two populations differed in their survivorship and selection responses to nicotine ingested by $M. sexta,$ their searching responses to tobacco, tomato, and other plants, and their searching responses to nicotine over a range of concentrations. Considering the historical abundance of a single host genus on a single plant species at U.M., the results of our work suggest that the U.M. population of **Cortesia congregata** has adapted to nicotine.

We suggest that local adaptations to plants occur when the net survival of a parasitoid species on hosts utilizing noxious plants is greater than that gained by avoiding such hosts, i.e., under conditions offering sufficient selective pressure. Therefore, we would not expect adaptations to plants to occur in populations in which several host species are usually available and parasitoid survival is adversely affected only when development occurs in a rare host feeding on one plant species. Likewise, we would not expect adaptations to plants to occur when a single host species is available on a diversity of plants and a relatively small proportion of the total host population is encountered on a noxious plant. However, we would expect local adaptations to plants to occur in populations in which the only available host or a consistently dominant and abundant host species is encountered on an abundant noxious plant species over time. Thus, local adaptations to abundant host species could lead to local adaptations to plants and these adaptations to plants, in turn, could lead to a higher degree of adaptation to specific hosts, as summarized in Table 5.

Although our predictions are based on the overall abundance of consistently available host and plant species over time, we note that these predictions may vary for unique situations of predictable but fluctuating conditions of host and plant abundance over both spatial and temporal dimensions. For example, some parasitoids utilize a single host genus that predictably occurs on a sequence of two or three different plants over a growing season, whereas other parasitoids utilize a single host genus that can simultaneously occur on different plants throughout the growing season. In the first case, the outcome would probably be a relatively homogeneous parasitoid population that is generally adapted to all of these plants, while in the second case, an alternative outcome may be the formation of subpopulations more highly adapted to single plant species.

Although host specificity of insect parasitoids is generally regarded as a desirable attribute for their use in biological control, we note that this taxon-based generalization may not hold. For example, parasitoid species with broad host ranges may be locally adapted to their most abundant host species or genera and the food plants on which these hosts are encountered and, thus, may be as effective as biological control agents as more host-specific parasitoid species. Similarly, host-specific parasitoids may be locally adapted to a specific abundant plant and may not be as effective as biological control agents when their hosts are located on different plants. Thus, populations may be functional specialists for specific herbivore hosts and/or the plants on which these hosts are encountered. If so, better predictions of biological control success may be made when the functional host and/or plant specificity of parasitoid populations is known or at least considered.

Local adaptations to the plants on which parasitoids typically encounter their hosts may explain some establishment failures but may also be exploited to enhance biological control efforts. For example, in classical biological control, parasitoids may be collected from one host on one plant species, colonized, then released to control the same host species or **congeners** on a different plant species. Given the plasticity of parasitoid for-

TABLE 5

Hypothesized Likelihood of Local Adaptations to Hosts and Plants in Interbreeding Population of Insect Parasitoids (H, Adaptations to Hosts Likely; P, Adaptations to Plants Likely; Parentheses Denote Some Degree of Adaptation)"

Relative local abundance of available herbivore host(s)	Relative local abundance of available food plants of herbivore host(s)		
	One plant	Several equally abundant plants[b]	One abundant plant/several
One Host"	H, P	H, —	H, (P)
Several equally abundant hosts*	—, P	- -	-, (P)
One abundant host/several	(H), P	(H), —	(H), (P)

[a] For parasitoid species restricted to a single host species or genus.
[b] Depending on the host and plant families involved, different outcomes are possible. For example, if available hosts utilize a diversity of noxious plants, parasitoid populations may be heterogeneous with subgroups that are adapted to specific plants or hosts.
[c] Only one host or plant is abundant but several are available.

aging behavior, this imported species may attack hosts on the new plant but its larval survival may be reduced and, thus, it may fail to establish. In this case, establishment could be encouraged by collecting parasitoids from hosts on the same plant or from a variety of plants which would provide more genetic heterogeneity. Adaptations to plants could also be encouraged through selective breeding when parasitoids are first colonized. Similarly, selective breeding for increased survival on a particular plant species or genotype may be used for augmentation of native or "immigrant" parasitoid populations.

ACKNOWLEDGMENTS

REFERENCES

Altahtawy, M. M., Hammad, S. M., and Hegazi, E. M. 1976. Studies on the dependence of *Microplitis rufiventris* Kok. (Hym., Braconidae) parasitizing *Spodoptera littoralis* (Bosd.) on own food as well as on food of its host. *Z. Angew. Entomol.* **83,** 3–13.

Altieri, M. A., Lewis, W. J., Nordlund, D. A., Gueldner, R. C., and Todd, J. W. 1981. Chemical interactions between plants and *Trichogramma* wasps in Georgia soybean fields. *Prot. Entomol.* **3,** 259–263.

Arthur, A. P. 1962. Influence of host tree on abundance of *Itoplectis conquisitor* (Say) (Hymenoptera: Ichneumonidae), a polyphagous parasite of the European pine shoot moth, *Rhyucionia* buoliana (Schiff) (Lepidoptera: Oleuthreutidae). *Can. Entomol. 94,* 337-347.

Arthur, A. P. 1966. Associative learning in *Itoplectis conquisitor* (Say) (Hymenoptera: Ichneumonidae). Can. *Entomol. 98, 213-223.*

Arthur, A. P. 1971. Associative learning by *Nemeritis canescens* (Hymenoptera: Ichneumonidae). Can. *Entomol.* 103, 1137-1141.

Baldwin, I. T. 1988. Short-term damage-induced increases in tobacco alkaloids protect plants. *Oecologia 75, 367-370.*

Barbosa, P., Gross, P., and Kemper, J. 1991. Influence of plant allelochemicals on the performance of the tobacco hornworm and its parasitoid, *Cotesia congregata. Ecology,* in press.

Barbosa, P., and Saunders, J. 1985. Plant allelochemicals: Linkages between herbivores and their natural enemies. *In* "Chemically Mediated Interactions between Plants and Other Organisms" (G. A. Cooper-Driver, T. Swain, and E. E. Conn, Eds.), pp. 107-137. Plenum, New York.

Barbosa, P., Saunders, J. A., Kemper, J., Trumbule, R., Olechno, J., and Martinat, P. 1986. Plant allelochemicals and insect parasitoids: The effects of nicotine on Cotesia *congregata* (Say) (Hymenoptera: Braconidae) and *Hyposoter annulipes* (Cresson) (Hymenoptera: Ichneumondiae). *J. Chem. Ecol.* 12, 1319-1328.

Beckendorf, S. K., and Hoy, M. A. 1985. Genetic improvement of arthropod natural enemies through selection, hybridization or genetic engineering techniques. *In* "Biological Control in Agricultural IPM Systems" (M. A. Hoy and D. C. Herzog, Eds.), pp. 167-187. Academic, New York.

Benn, M., DeGrave, J., Gnanasunderam, C., and Hutchins, R. 1979. Host-plant pyrrolizidine alkaloids in *Nyctemera annulata* Borsd: Their persistence through the life cycle and transfer to a parasite. *Experientia 35,* 731-732.

Bentz, J., and Barbosa, P. 1990. Effects of dietary nicotine (0.1%) and parasitism by *Cotesia congregata* on the growth and food consumption and utilization of the tobacco hornworm, Munduca *sexta. Entomol. Exp. Appl. 57, 1-8.*

Bergman, J. M., and Tingey, W. M. 1979. Aspects of interaction between plant genotypes and biological control. *Bull. Entomol. Soc. Amer.* **25,** 275–279.

Blumberg, D., and DeBach, P. 1979. Development of *Habrolepsis rouxi* Compere (Hymenoptera: Encyrtidae) in two armored hosts (Homoptera: Diaspididae) and parasite egg encapsulation by California red scale. *Ecol. Entomol. 4, 299-306.*

Boethel, D. J., and Eickenbary, R. D. (Eds.) 1986. "Interaction of Plant Resistance and Parasitoids and Predators of Insects." Ellis Horwood, Chichester.

Bombosch, S. 1966. Occurrence of enemies on different weeds with aphids. In "Ecology of Aphidophagous Insects" (I. Hodek, Ed.), pp. 177-179. Junk, The Hague.

Bouletreau, M., and David, J. R. 1981. Sexually dimorphic response to host habitat toxicity in *Drosophila* parasitic wasps. *Evolution 35, 395-399.*

Bush, G. L. 1969. Sympatric host race formation and speciation in frugivorous flies of the genus *Rhagoletis* (Diptera, Tephritidae). *Evolution 23,* 237-251.

Campbell, B. C., and Duffey, S. S. 1979. Tomatine and parasitic wasps: Potential incompatibility with biological control. *Science* 205, 700-702.

Carton, Y., Bouletreau, M., van Alphen, J. J. M., and van Lenteren, J. C. 1986. The Drosophila parasitic wasps. *In* "The Genetics and Biology of Drosophila," Vol. 3. Academic Press, London.

Cheng, L. 1970. Timing of attack by *Lypha dubia* Vall. (Diptera: Tachinidae) on the winter moth, *Operophtheru brumata* (Lepidoptera: Geometridae) as a factor affecting parasitoid success. *J. Anim. Ecol. 39,* 313–320.

Corbet, S. A. 1985. Insect chemosensory responses: A chemical legacy hypothesis. *Ecol. Entomol.* 10, 143–153.

Ding, D., Swedenborg, P. D., and Jones, R. L. 1989a. Chemical stimuli in host-seeking behavior of *Mucrocentrus grandii* Goidanich (Hymenoptera: Braconidae). *Ann. Entomol. Soc. Amer. 82, 232-236.*

Ding, D., Swedenborg, P. D., and Jones, R. L. 1989b. Plant odor preferences and learning in *Macrocentrus grandii* (Hymenoptera: Braconidae), a larval parasitoid of the European corn borer, *Ostrinia nubilalis* (Lepidoptera: Pyralidae). *J. Kans. Entomol. Soc. 62,* 164-176.

Dmoch, J., Lewis, W. J., Martin, B. P., and Nordlund, D. A. 1985. Role of host-produced stimuli and learning in host selection behavior of *Cotesiu* (= *Apanteles) marginiuentris* (Cresson) (Hymenoptera, Braconidae). *J. Chem. Ecol.* 11, 453-463.

Drost, Y. C., Lewis, W. J., Zanen, P. O., and Keller, M. A. 1986. Beneficial arthropod behavior mediated by airborne semiochemicals. I. Flight behavior and influence of preflight handling of *Microplitis croceipes* (Cresson). *J. Chem. Ecol.* 12, 1247-1262.

Drost, Y. C., Lewis, W. J., and Tumlinson, J. H. 1988. Beneficial arthropod behavior mediated by airborne semiochemicals. V. Influence of rearing method, host plant, and adult experience on host-searching behavior of *Microplitis croceipes* (Cresson), a larval parasitoid of Heliothis. *J. Chem. Ecol.* 14, 1607-1616.

Elzen, G. W., Williams, H. J., and Vinson, S. B. 1983. Response by the parasitoid *Campoletis sonorensis* (Hymenoptera: Ichneumonidae) to chemicals (synomes) in plants: Implications for host habitat location. *Environ. Entomol.* 12, 187221876.

Elzen, C. W., Williams, H. J., and Vinson, S. B. 1984a. Isolation and identification of cotton synomes mediating searching behavior by the parasitoid *Campoletis sonorensis. J. Chem. Ecol.* **10,** 1251–1264.

Elzen, G. W., Williams, H. J., and Vinson, S. B. 1984b. Role of diet in host selection of *Heliothis virescens* by parasitoid *Campoletis sonorensis* (Hymenoptera: Ichneumonidae). *J. Chem. Ecol.* 10, 1525–1541.

Flanders, S. E. 1942. Abortive development in parasitic Hymenoptera, induced by the food plant of the insect host. *J. Econ. Entomol.* **35,** 834–835.

Fox, L. R., and Morrow, P. A. 1981. Specialization: Species property or local phenomenon? *Science 2* **11,** 887–893.

Gilmore, J. U. 1938a. Observations on the hornworm attacking tobacco in Tennessee and Kentucky. *J. Econ. Entomol.* **31,** 706–712.

Gilmore, J. U. 1938b. Notes on *Apanteles congregatus* (Say) as a parasite in tobacco hornworms. *J. Econ. Entomol.* 31, 712-715.

Gleason, H. A., and Cronquist, A. 1963. "Manual of Vascular Plants of Northeastern United States and Canada," Willard Grant Press, Boston.

Gunasena, G. H., Vinson, S. B., and Williams, H. J. 1990. Effects of nicotine on growth, development and survival of the tobacco budworm (Lepidoptera: Noctuidae) and the parasitoid *Campoletis sonorensis* (Cameron) (Hymenoptera: Ichneumonidae). *Econ. Entomol. 83, 1777-1782.*

Harrington, E. A., and Barbosa, P. 1978. Host habitat influences on oviposition by *Parasetigena silvestris* (R-D), a larval parasite of the gypsy moth. *Environ. Entomol. 7, 466-468.*

Haynes, D. L., and Butcher, J. W. 1962. Studies on host preference and its influence on European pine shoot moth success and development. *Can. Entomol.* **94,** 690–706.

Hérard, F., Keller, M. A., Lewis, W. J., and Tumlinson, J. H. 1988a. Beneficial arthropod behavior mediated by airborne semiochemicals. III. Influence of age and experience on flight chamber responses of *Microplitis demolitor* Wilkinson. *J. Chem. Ecol.* 14, 1583-1596.

Hérard, F., Keller, M. A., Lewis, W. J., and Tumlinson, J. H. 1988b. Beneficial arthropod behavior mediated by airborne semiochemicals. IV. Influence of host diet on host-oriented flight chamber responses of *Microplitis demolitor* Wilkinson. *J. Chem. Ecol.* 14, 1597-1606.

Herrebout, W. M., and van der Veer, J. *1969. Encarceliu rutilla* Vill. III. Preliminary results of olfactometer experiments with females of known age. *Z. Angew. Entomol.* **64,** 55–61.

Hodges, R. W. 1971. "The Moths of America North of Mexico, Fasc. 21, Sphingoidea." E. W. Classey, Middlesex.

Jaenike, J. 1983. Induction of host preference in *Drosophila melanogaster. Oecologiu 58, 320-325.*

Jaenike, J. 1988. Effects of early adult experience *on* host selection in insects: Some experimental and theoretical results. *J. Insect Behav.* 1,3-15.

Jones, D. A., Parsons, J., and Rothschild, M. 1962. Release of hydrocyanic acid from crushed tissues of all stages in the life cycle of species of the Zygaeninae (Lepidoptera). *Nature* 193, 52–53.

Kaas, J. P., Elzen, G. W., and Ramaswamy, S. B. 1990. Learning in *Microplitis croceipes* (Hym, Braconidae). *J. Appl. Entorrwl.* 109, 268-273.

Kaiser, L., Pham-Delegue, M. H., and Masson, C. 1989. Behavioral study of plasticity in host preferences of *Trichogrumma maidis* (Hym.: Trichogrammatidae). *Physiol. Entomol.* 14, 53-60.

Kester, K. M., and Barbosa, P. 1991. Post-emergence learning in the insect parasitoid, *Cotesia congregata. J. Insect Behav. 4, 727-742.*

Krombein, K. V., Hurd, P. D., Jr., Smith, D. R., and Burks, B. D. 1979. "Catalog of Hymenoptera in America North of America," p. 245. Smithsonian Institution, Washington, D. C.

Lecomte, C., and Thibout, E. 1984. Etude olfactometrique de l'action de diverses substances allelochimiques végétales dans la recherche de l'hôte par *Diadromus pulchellus* (Hymenoptera: Ichneumonidae). *Entomol. Exp. Appl. 35, 295-303.*

Lewis, W. J., and Tumlinson, J. H. 1988. Host detection by chemically mediated associative learning in a parasitic wasp. *Nature* 331, 257-259.

Lewis, W. J., and Takasu, K. 1990. Plastic use of learned odors by a parasitic wasp in accordance with host and food needs. *Nature* **348,** 635–636.

Lewis, W. J., Vet, L. E. M., Tumlinson, J. H., van Lenteren, J. C., and Papaj, D. R. 1990. Variations in parasitoid foraging behavior: Essential element of a sound biological control theory. *Environ. Entomol.* 19, 1183-1193.

Luck, R. F., and Uygun, N. 1986. Host recognition and selection by *Aphytis* species: Response to California red, oleander, and cactus scale cover extracts. *Entomol. Exp. Appl. 40,* 129-136.

Martin, P. B., Lingren, P. D., Green, G. L., and Ridgeway, R. L. 1976. Parasitization of two species of Plusiinae and *Heliothis* spp. after releases of *Trichogramma pretiosum* in seven crops. *Environ. Entomol.* **5,** 991–995.

McAuslane, H. J., Vinson, S. B., and Williams, H. J. 1990. Influence of host plant on mate location by the parasitoid *Campoletis sonorensis* (Hymenoptera: Ichneumonidae). Environ. Entomol. 19, 26-31.

Mehta, C. R., and Patel, N. R. 1983. A network algorithm for the exact treatment of Fischer's exact test in R X C contingency tables. *J. Amer. Stat. Assoc.* **78,** 427–434.

Mohyuddin, A. I., Inayatullah, C., and King, E. G. 1981. Host selection and strain occurrence in *Apanteles flavipes* (Cameron) (Hymenoptera: Braconidae) and its bearing on biological control of graminaceous stem-borers (Lepidoptera: Pyralidae). *Bull. Entomol. Res.* **71,** 575–581.

Monteith, L. G. 1955. Host preferences of *Drino bohemica* Mesn. with particular reference to olfactory responses. Can. *Entomol.* **87,** 509–530.

Monteith, L. G. 1958. Influence of host and its food plant on host-finding by *Drino bohemica* Mesn. and interaction of other factors. *Proc. Znt. Congr. Entomol. 10th 2, 603-606.*

Monteith, L. G. 1963. Habituation and associative learning in *Drino bohemica* Mesn. (Diptera: Tachinidae). *Can. Entomol.* **95,** 418–426.

Morgan, A. C. 1910. Observations recorded at the 236th regular meeting of the Entomological Society of Washington. *Proc. Entomol. Soc. Wash.* 12, 72.

Narayanan, E. S., and Subba Rao, B. R. 1955. Studies in insect parasitism. III. The effects of different hosts on the physiology, on the development and behavior and on the sex ratio of *Microbracon gelechiae* Ashmead (Hymenoptera: Braconidae). *Beitr. Entomol.* **5,** 36–60.

Nettles, W. C. 1979. *Encelatoria* sp. females: Factors influencing response to cotton and okra plants. *Environ. Entomol. 8,* 619-623.

Nettles, W. C. 1980. Adult *Eucelatoriu* sp.: Response to volatiles from cotton and okra plants and from larvae of *Heliothis* virescens, *Spodoptera eridania* and *Estigmene acrea. Environ. Entomol. 9, 759-763.*

Nishida, T. 1956. An experimental study of the ovipositional behavior of *Opius fletcheri* Silvestri (Hymenoptera: Braconidae), a parasite of the melon fly. *Proc. Hawaii. Entomol. Soc.* 16, 126-134.

Nordlund, D. A., Lewis, W. J., and Altieri, M. A. 1988. Influence of plant-derived semiochemicals on host/prey selection behavior of

entomophagous insects. *In* "Novel Aspects of Insect-Plant Interactions" (P. Barbosa and D. K. Letourneau, Eds.), pp. 65–90. Wiley, New York.

Nordlund, D. A., and Sauls, C. E. 1981. Kairomones and their use for the management of entomophagous insects. IX. Effect of host plants on kairomonal activity of frass of *Heliothis zea* larvae for the parasitoid *Microplitis croceipes. J. Chem. Ecol.* '7, 1057-1061.

Papaj, D. R., and Prokopy, R. J. 1986. Phytochemical basis of learning in *Rhagoletis pomonella* and other herbivorous insects. *J. Chem. Ecol.* 12, 1125-1143.

Papaj, D. R., and Prokopy, R. J. 1988. The effect of prior adult experience on components of habitat preference in the apple maggot fly *(Rhagoletis pomonella). Oecologia 76, 538-543.*

Parr, J. C., and Thurston, R. 1972. Toxicity of nicotine in synthetic diets to larvae of the tobacco hornworm. *Ann. Entomol. Soc. Amer.* 65, 1185–1188.

Pimentel, D. 1966. Wasp parasite *(Nasonia uitripennis)* survival on its house fly host *(Musca* domestica) reared on various foods. *Ann. Entomol. Soc. Amer.* 59, 1031-1038.

Prevost, G., and Lewis, W. J. 1990. Genetic differences in the response of *Microplitis croceipes* to volatile semiochemicals. *J. Znsect Behav.* 3, 277–287.

Price, P. W. 1975. Reproductive strategies of parasitoids. *In* "Evolutionary Strategies of Parasitic Insects and Mites," pp. 87-111. Plenum, New York.

Price, P. W. 1980. "Evolutionary Biology of Parasites." Princeton University, Princeton.

Price, P. W., Bouton, C. E., Gross, P., McPherson, B. A., Thompson, J. N., and Weis, A. E. 1980. Interactions among three trophic levels: Influence of plants and interactions between insect herbivores and natural enemies. *Annu. Rev. Ecol. Syst.* 11, 41-65.

Read, D. P., Feeny, P. P., and Root, R. B. 1970. Habitat selection by the aphid parasite *Diaeretiella rapae* (Hymenoptera: Braconidae) and hyperparasite *Charips brassicae* (Hymenoptera: Cynipidae). *Can. Entomol.* 102, 1597–1578.

Reichstein, T., von Euw, J., Parson, J. A., and Rothschild, M. 1968. Heart poisons in the monarch butterfly. *Science* 161, 861–866.

Roth, J. P., King, E. G., and Thompson, E. 1978. Host location behavior by the tachinid, *Lixophaga diatraeae. Enuiron. Entomol.* 7, 794–798.

Rothschild, M., Valadon, G., and Mummer, R. 1977. Carotenoids of the pupae of the large white butterfly *(Pieris brassicae)* and the small white butterfly *(Pieris rapae). J. Zool.* 181, 323–339.

Salt, G. 1958. Parasite behavior and the control of insect pests. *Endeavor 65,* 145–148.

Sandlan, K. 1980. Host location by *coccygomimus turnionella* (Hymenoptera: Ichneumondiae). *Entomol. Exp. Appl.* 27, 233–245.

SAS Institute. 1985. "SAS User's Guide: Statistics, Version 5 Edition." SAS Institute, Cary.

Sauls, C. E., Nordlund, D. A., and Lewis, W. J. 1979. Kairomones and their use for the management of entomophagous insects. VIII. Effects of diet on the kairomonal activity of frass from *Heliothis zea* (Boddie) larvae for *Microplitis croceipes* (Cresson). *J. Chem. Ecol.* 5, 363–369.

Sekhar, P. S. 1960. Host relationships of *Aphidius testaceipes* (Cresson) and *Praon aguti* (Smith), primary parasites of aphids. Can. *J. Zool.* 38, 593–603.

Self, L. S., Guthrie, F. E., and Hodgson, E. 1964. Adaptation of tobacco hornworms to the ingestion of nicotine. *J. Insect Physiol.* 10, 907–914.

Shahjahan, M. 1974. *Eigeron* flowers as a food and attractive odor

source for *Peristenus pseudopallipes,* a braconid parasitoid of the tarnished plant bug. *Environ. Entomol. 3, 69-72.*

Sheehan, W., and Shelton, A. M. 1989. The role of experience in plant foraging by the aphid parasitoid *Diaeretiella rapae* (Hymenoptera: Aphidiidae). *J. Znsect Behav. 2, 743-759.*

Smith, D. A. S. 1978. Cardiac glycosides in *Danaus chrysippus* (L.) provide some protection against an insect parasitoid. *Experientia* 34, 844–846.

Smith, J. M. 1957. Effects of the food plant of California red scale, *Aonidiella aurantii* (Mask), on reproduction of its hymenopterous parasites. *Can. Entomol. 89,* 219–230.

Smith, M. J. 1987. When learning guides evolution. *Nature* 329, 761–762.

Streams, F. A., Shahjahan, M., and LeMeasurier, H. G. 1968. Influence of plants on the parasitization of the tarnished plant bug by *Leiophron pallipes. J. Econ. Entomol. 6* 1, 996-998.

Taylor, R. J. 1974. Role of learning in insect parasitism. *Ecol. Monogr.* 44, 89–104.

Thompson, A. C., Roth, J. P., and King, E. G. 1983. Larviposition kairomone of the tachinid *Lixophaga diatraeae. Environ. Entomol.* 12, 1312–1314.

Thorpe, K., and Barbosa, P. 1986. Effects of consumption of high and low nicotine tobacco by *Manduca sexta* (Lepidoptera: Sphingidae) on the survival of the gregarious parasitoid *Cotesia congregata* (Hymenoptera: Braconidae). *J. Chem. Ecol.* 12, 1329-1337.

Thorpe, W. N., and Candle, H. B. 1938. A study of the olfactory responses of insect parasites to the food plant of their host. *Parasitology 30, 523-528.*

Thorpe, W. J., and Jones, F. G. W. 1937. Olfactory conditioning in a parasitic insect and its relation to the problem of host selection. *Proc. R. Soc. London B* 124, 56–81.

Thurston, R., and Fox, P. M. 1972. Inhibition by nicotine of emergence of *Apanteles congregatus* from its host, the tobacco hornworm. *Ann. Entomol. Soc. Amer. 65,* 547–550.

Tietz, H. M. 1972. "An Index to the Described Life Histories, Early Stages and Hosts of the Macrolepidoptera of the Continental United States and Canada." Allyn Museum, Sarasota.

Turlings, T. C. J., Tumlinson, J. H., and Lewis, W. J. 1991. Exploitation of herbivore-induced plant odors by host-seeking parasitic wasps. *Science* 250, 1251–1253.

Turlings, T. C. J., Tumlinson, J. H., Lewis, W. J., and Vet, L. E. M. 1989. Beneficial arthropod behavior mediated by air-borne semiochemicals. VII. Learning of host-related odors induced by a brief contact experience with host by-products in *Cotesia marginiventris* (Cresson), a generalist larval parasitoid. *J. Znsect Behav. 2,* 217-225.

van Alphen, J. J. M., and Vet, L. E. M. 1986. An evolutionary approach to host finding and selection. *In* "Insect Parasitoids" (J. Waage and D. Greathead, Eds.), pp. 23-61. Academic Press, New York.

Vet, L. E. M. 1983. Host-habitat location through olfactory cues by *Leptopilina clavipes* (Hartig) (Hym: Eucoilidae), a parasitoid of fungivorous *Drosophila:* The influence of conditioning. *Neth. J. Zool.* 33, 225–248.

Vet, L. E. M., and Janse, C. J. 1984. Fitness of two siblings species of *Asobara* (Braconidae: Alysiinae), larval parasitoids of Drosophilidae in different microhabitats. *Ecol. Entomol. 9, 345-354.*

Vet. L. E. M., Janse, C. J., van Achterberg, C., and van Alphen, J. J. M. 1984. Microhabitat location and niche segregation in two sibling species of Drosophilid parasitoids: *Asobara tabida* (Nees) and *A. rufescens* (Foerster) (Braconidae: Alysiinae). *Oecologia 61,* 182–188.

Vet, L. E. M., and van Opzeeland, K. 1984. The influence of conditioning on olfactory microhabitat and host location in *Asobara tabida* (Nees) and *A. rufescens* (Foerster) (Braconidae: Alysiinae) larval parasitoids of Drosophilidae. *Oecolgia* 63, 171-177.

Vet, L. E. M., and van Opzeeland, K. 1985. Olfactory microhabitat selection in *Leptopilina heterotoma* (Thomson) (Hym.: Eucoilidae), a parasitoid of Drosophilidae. *Neth. J. Zool. 35, 496-504.*

Vet, L. E. M., Lewis, W. J., Papaj, D. R., and van Lenteren, J. C. 1990. A variable-response model for parasitoid foraging behavior. *J. Insect Behav. 3, 471-490.*

Vinson, S. B. 1975. Biochemical coevolution between parasitoids and their hosts. *In* "Evolutionary Strategies of Parasitic Insects and Mites" (P. W. Price, Ed.), pp. 14-48. Plenum, New York.

Vinson, S. B. 1976. Host selection by insect parasitoids. *Annu. Reu. Entomol. 2 1, 109-133.*

Vinson, S. B. 1981. Habitat location. In "Semiochemicals: Their Role in Pest Control" (D. A. Nordlund, R. L. Jones, and W. J. Lewis, Eds.), pp. 51-77. Wiley, New York.

Vinson, S. B. 1984. The behavior of parasitoids. In "Insect Physiology, Biochemistry and Pharmacology" (G. A. Kerkut and L. I. Gilbert, Eds.), pp. 417-469. Pergamon, New York.

Vinson, S. B., Barfield, C. S., and Henson, R. D. 1977. Oviposition behavior of *Bracon mellitor,* a parasitoid of the boll weevil (*Anthonomus grandis).* II. Associative learning. *Physiol. Entomol. 2,* 157–164.

Walker, M. G. 1940. Notes on the distribution of *Cephus pygmaeus* Linn. and its parasite *Collyria calcitrator* Grav. *Bull. Entomol. Res.* **30,** 551–573.

Wardle, A. R., and Borden, J. H. 1985. Age-dependent associative learning by *Eneristes roborutor* (F.). *Can. Entomol.* 117, 605–616.

Wardle, A. R., and Borden, J. H. 1989. Learning of an olfactory stimulus associated with a host microhabitat by *Exeristes roborator. Entomol. Exp. Appl.* **52,** 271–279.

Whitman, D. W. and Eller, F. J. 1990. Parasitic wasps orient to green leaf volatiles. *Chemoecology* 1, 69-75.

Williams, H. J., Elzen, G. W., and Vinson, S. B. 1988. Parasitoid-host-plant interactions, emphasizing cotton *(Gossypium). In* "Novel Aspects of Insect-Plant Interactions" (P. Barbosa and D. K. Letourneau, Eds.), pp. 171–200. Wiley, New York.

Young, J. H., and Price, R. G. 1975. Incidence, parasitism and distribution patterns of *Heliothis zea* on sorghum, cotton and alfalfa of southwestern Oklahoma. *Environ. Entomol. 4, 777-779.*

Zehnder, G. W., and Trumbule, J. T. 1984. Host selection of *Liriomyza* species (Diptera: Agromyzidae) and associated plantings of tomato and celery. *Environ. Entomol.* 13, 492–496.

Zhody, N. 1976. On the effect of the food of *Myzus persicae* Sulz. on the hymenopterous parasite, *Aphelinus asychis* Walker. *Oecologia* 26, 185-191.

Zwolfer, H., and Kraus, M. 1957. Biocoenotic studies of the parasites of two fir- and two oak-tortricids. *Entomophugu* **2,** 173–196.