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PLANT-NATURAL ENEMY ASSOCIATION IN THE TRITROPHIC SYSTEM *Cotesia rubecula–Pieris rapae*–BRASSICACEAE (CRUCIFERAE): II. PREFERENCE OF *C. rubecula* FOR LANDING AND SEARCHING

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Abstract—The responses of the parasitoid *Cotesia rubecula* to differently damaged cabbages were recorded during a series of choice tests. To determine if flying *C. rubecula* can discriminate differences in the blend of volatiles emitted by cabbages damaged by different causes and how plant volatiles released from a distant source affect the searching behavior of *C. rubecula* once searching on a plant, wasps were presented with a choice of plants located one behind the other and separated by a distance of 15 cm. The sources of damage were: cabbage damaged by the host (*Pieris rapae*), by a nonhost lepidopteran herbivore (*Plutella xylostella*), by a nonhost, noninsect herbivore (snail), and by mechanical means. The results showed that the site of first landing and the time spent searching on the leaves was influenced by the type of damage inflicted on plants. Wasps preferred to land on cabbages damaged by host and nonhost species of Lepidoptera over those damaged by snails and mechanical means. No preference was observed for first landing between cabbages damaged by the two species of Lepidoptera or between cabbages damaged by snails and mechanical means. Cabbage damaged by *P. rapae* was searched most intensively, followed by cabbage damaged by *P. xylostella*, cabbage damaged by snails, and cabbage damaged by mechanical means. *C. rubecula* differentiates between the volatile blends emitted by differently damaged cabbages, and it is attracted to volatiles related to recent lepidopteran damage. Wasps searched longer on freshly damaged than on leaves with older damage.

Key Words—*Cotesia rubecula*, Hymenoptera, Braconidae, Lepidoptera, Pieridae, Plutellidae, *Pieris rapae*, *Plutella xylostella*, *Helix aspera*, *Brassica*

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oleracea, Phaseolus vulgaris, tritrophic interactions, synomones, infochemicals.

INTRODUCTION

The host plant has become one of the main components examined in studies of interactions between insect herbivores and their natural enemies. Increasing evidence suggests that the host plant is the main provider of airborne chemicals utilized by natural enemies to locate their hosts or prey (Vinson, 1975, 1984; Auger et al., 1989; Ramachandran et al., 1991; Dicke et al., 1990a,b; Turlings et al., 1990, 1991; Whitman and Eller, 1990; Dicke and Takabayashi, 1991). Although the idea of chemical communication between the natural enemies of herbivores and plants was discussed by Price et al. (1980), only recently has chemical evidence of that communication been provided. Identification of the volatile compounds emitted by infested plants showed that these compounds are plant chemicals and that feeding by herbivorous insects can induce plants to release a blend of volatile chemicals different from that released during the intact state or when mechanically damaged (Dicke et al., 1990a,b; Turlings et al., 1990, 1991; Whitman and Eller, 1990; Dicke and Takabayashi, 1991). Natural enemies can perceive these differences and prefer to search plants that are damaged by their herbivorous hosts or prey (Dicke et al., 1990a; Turlings et al., 1990; Steinberg et al., 1993).

The aim of the present study was to investigate further the involvement of plant volatile chemicals in the searching behavior of the parasitoid *Cotesia rubecula* (Marshall) (Hymenoptera: Braconidae). *C. rubecula* is a solitary endoparasitoid of a number of lepidopteran species that feed on cabbage, with a preference for *Pieris rapae* L. as the host species (Lepidoptera: Pieridae) (Shenefelt, 1972). Females of *C. rubecula* are attracted from a distance to volatiles emitted by cabbage infested by *P. rapae* (Nealis, 1986; Keller, 1990; Kaiser and Cardé, 1992). Volatile compounds related to damaged cabbage attract *C. rubecula* (Agelopoulos and Keller, 1994). Females are attracted to cabbage damaged by mechanical means, *P. rapae*, *Plutella xylostella* L. (Lepidoptera: Plutellidae, a nonhost herbivore), and snails (*Helix aspera* Müler, a nonhost, noninsect herbivore). *C. rubecula* is also attracted to mechanically damaged, nonhost plant species (bean and geranium), frass and regurgitate of *P. rapae*, frass of *P. xylostella*, but not to isolated larvae of *P. rapae* or intact cabbage, bean, and geranium.

Although we showed that *C. rubecula* is attracted to volatile chemicals from damaged cabbage, it was not determined in our previous study if the parasitoid responds differently to the volatile blends from different kinds of damaged plants. To investigate this matter, a novel choice test was developed to investigate differences in the responses of *C. rubecula* to different types of plant damage.

METHODS AND MATERIALS

Culturing of plants and insects and their handling during experiments were the same as described in Agelopoulos and Keller (1994).

Experimental Procedure. Two plants were arranged inside a wind tunnel (Keller, 1990) in a series (one behind the other), separated by a distance of 15 cm (Figure 1). The releasing tube (Agelopoulos and Keller, 1994) was placed 80 cm away from the downwind plant. The advantage of a serial test over a conventional parallel choice test is that plants arranged in a series produce a differential distribution of infochemicals inside the wind tunnel, and the space of the wind tunnel can be separated into three parts. Part A is the space between the releasing tube and the downwind plant where the air conveys information from both plants. Part B is the space between the downwind plant and the upwind plant where the air conveys information only from the upwind plant. Part C is the remainder of the wind tunnel where the air conveys no information. The preference of the flying female during the first landing is related to similarities or differences in the blend of volatile compounds emitted by the two plants. The time spent on the damaged leaf of each plant is related to stimuli encountered on the damaged leaves and to volatile chemicals that the air conveys. When searching on the downwind plant, the decision to fly further is related to stimuli encountered on the damaged leaf and volatile chemicals released from the upwind plant. When on the upwind plant, the decision to fly further is related to stimuli present on the damaged leaf only.

The movements and the behavior of a female during a test were recorded on video tape and subsequently analyzed using an event recorder (The Observer 2.0; Noldus, 1991). The maximum time of an observation was set at 10 min after the release of the insect. Thirty experienced females (see Agelopoulos and Keller, 1994) were tested for every pair of plants. To understand how the

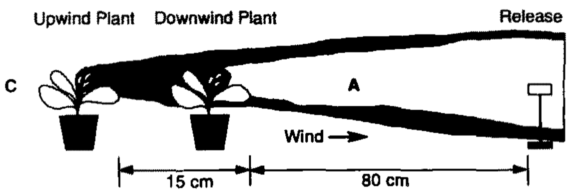

FIG. 1. Design of the serial choice test showing the distribution of plumes of volatile infochemicals from damaged leaves. A wasp in region A receives volatiles from both plants, in region B from the upwind plant only, and in region C from neither plant.

arrangement of the two plants (upwind vs. downwind) influences the movements of female wasps, 15 females were tested in one arrangement and 15 in the alternative arrangement. During an experimental day both arrangements were tested. The plant arrangement was changed every second observation. The cabbage plants used for an experiment were all of the same stage (seven leaves), while beans (*Phaseolus vulgaris* L.) had four leaves. The damage was restricted to only one leaf of the plant. Care was taken to ensure that the same amount of damage was present on each plant used for a test. During an experimental day, treated plants were replaced every hour. The wind speed was 54.3 cm/sec and the experiments took place between 8:00 AM and 12:00 noon. The components of behavior analyzed were the plant chosen for the first landing, the time spent on each damaged leaf during the first evaluation, and the overall time spent on the damaged leaf of each plant after multiple visits. For some females the first evaluation of a plant took place in one visit while for others the first evaluation took place in more than one visit. The first evaluation was defined as the time of all the visits (one or more) that females exhibited during their first encounter with a plant.

Treatments. Choice tests were separated into four groups (Table 1). In group A, the objective was to observe preferences of *C. rubecula* between mechanically damaged cabbages and those damaged by herbivores. In group B, the aim was to observe preferences of *C. rubecula* for cabbages damaged by different herbivores. In group C, the aim was to examine the effects of the age of damage on the preference of females. In group D, the objective was to record the responses of *C. rubecula* to mechanically damaged cabbage or bean (nonhost plant). The herbivores that damaged the cabbage plants were: *P. rapae* (host), *P. xylostella* (nonhost lepidopteran), and snails (*H. aspera*, a nonhost, noninsect herbivore). To obtain cabbage damage by lepidopteran larvae, 10 second instars of *P. rapae* or 10 fourth instars of *P. xylostella* were isolated on one leaf and left to feed for 24 hr. During this time the larvae consumed approximately 2 cm^2 of leaf tissue. Prior to the experiment the larvae and their by-products were removed and the plant was washed with water. To control the amount of damage done by snails, they were observed while feeding and removed when they had devoured approximately the same amount of leaf area as the other herbivores. After the removal of snails, the plant was washed. Mechanical damage was caused by removal of 2 cm^2 from the leaf using a razor blade.

Based on the time that the damage was inflicted on the plant, three different categories of damage were defined: fresh, recent, and old. Fresh damage was defined as the damage caused before the commencement of the tests such as mechanical damage on cabbage and bean and damage caused by snails. Recent damage was defined as the damage caused by *P. rapae* or *P. xylostella* after 24 hr of infestation. Old damage was obtained by holding a freshly damaged or

TABLE 1. RESPONSES OF *C. rubecula* TO CABBAGE DAMAGED BY DIFFERENT MEANS IN SERIAL CHOICE TEST[a]

Comparison		Downwind plant	Upwind plant
A. Mechanically-damaged cabbage vs. cabbage damaged by herbivores			
Fresh mechanical A vs. fresh mechanical B	I. Plant arrangement	Fresh mechanical A	Fresh mechanical B
	First landing (no.)	15	0
	Duration of first evaluation (min)[b]	0.79 ± 0.09^{c}	0.04 ± 0.03
	Overall time on damaged leaf (min)	0.79 ± 0.09^{c}	0.04 ± 0.03
	II. Plant arrangement	Fresh mechanical B	Fresh mechanical A
	First landing (no.)	13	0
	Duration of first evaluation (min)	1.38 ± 0.30^{c}	0.42 ± 0.22
	Overall time on damaged leaf (min)	1.61 ± 0.33^{c}	0.42 ± 0.22
	Preferred site of first landing	Downwind plant	
	Comparison of "first evaluation" between arrangements	Fresh mechanical A ns Fresh mechanical B[c]	
Fresh mechanical vs. recent *P. rapae*	I. Plant arrangement	Fresh mechanical	Recent *P. rapae*
	First landing (no.)	5	10
	Duration of first evaluation (min)	0.72 ± 0.29^{c}	4.45 ± 0.94
	Overall time on damaged leaf (min)	1.05 ± 0.33^{c}	7.07 ± 0.46
	II. Plant arrangement	Recent *P. rapae*	Fresh mechanical
	First landing (no.)	15	0
	Duration of first evaluation (min)	6.50 ± 0.88^{c}	0.41 ± 0.22
	Overall time on damaged leaf (min)	7.82 ± 0.43^{c}	0.41 ± 0.22
	Preferred site of first landing	Recent *P. rapae*	
	Comparison of "first evaluation" between arrangements	Fresh mechanical ns recent *P. rapae*[c]	
Fresh mechanical vs. recent *P. xylostella*	I. Plant arrangement	Fresh mechanical	Recent *P. xylostella*
	First landing (no.)	4	11
	Duration of first evaluation (min)	0.31 ± 0.07^{c}	2.27 ± 0.58
	Overall time on damaged leaf (min)	0.40 ± 0.11^{c}	4.94 ± 0.68
	II. Plant arrangement	Recent *P. xylostella*	Fresh mechanical
	First landing (no.)	15	0
	Duration of first evaluation (min)	3.65 ± 0.39^{c}	0.96 ± 0.19
	Overall time on damaged leaf (min)	5.57 ± 0.43^{c}	1.06 ± 0.24
	Preferred site of first landing	Recent *P. xylostella*	
	Comparison of "first evaluation" between arrangements	Fresh mechanical ns Recent *P. xylostella* ns	

TABLE 1. CONTINUED

Comparison		Downwind plant	Upwind plant
A. Mechanically-damaged cabbage vs. cabbage damaged by herbivores			
Fresh mechanical vs. fresh snail	I. Plant arrangement	Fresh mechanical	Fresh snail
	First landing (no.)	15	0
	Duration of first evaluation (min)	2.70 ± 0.54 ns	2.14 ± 0.50
	Overall time on damaged leaf (min)	3.30 ± 0.55 ns	2.14 ± 0.50
	II. Plant arrangement	Fresh snail	Fresh mechanical
	First landing (no.)	14	1
	Duration of first evaluation (min)	2.12 ± 0.38 ns	1.87 ± 0.63
	Overall time on damaged leaf (min)	2.14 ± 0.64 ns	2.75 ± 0.40
	Preferred site of first landing	Downwind	
	Comparison of "first evaluation" between arrangements	Fresh mechanical ns Fresh snail ns	
B. Damage by different herbivores			
Recent *P. rapae* A vs. recent *P. rapae* B	I. Plant arrangement	Recent *P. rapae* A	Recent *P. rapae* B
	First landing (no.)	13	2
	Duration of first evaluation (min)	6.62 ± 0.78[c]	1.44 ± 0.57
	Overall time on damaged leaf (min)	6.84 ± 0.62[c]	1.44 ± 0.57
	II. Plant arrangement	Recent *P. rapae* B	Recent *P. rapae* A
	First landing (no.)	11	4
	Duration of first evaluation (min)	6.08 ± 0.62[c]	1.25 ± 0.64
	Overall time on damaged leaf (min)	6.17 ± 0.95[c]	2.68 ± 0.77
	Preferred site of first landing	Downwind	
	Comparison of "first evaluation" between arrangements	Recent *P. rapae* A[c] Recent *P. rapae* B[c]	
Recent *P. rapae* vs. recent *P. xylostella*	I. Plant arrangement	Recent *P. rapae*	Recent *P. xylostella*
	First landing (no.)	13	2
	Duration of first evaluation (min)	5.79 ± 0.87[c]	0.65 ± 0.24
	Overall time on damaged leaf (min)	7.69 ± 0.44[c]	0.71 ± 0.25
	II. Plant arrangement	Recent *P. xylostella*	Recent *P. rapae*
	First landing (no.)	14	1
	Duration of first evaluation (min)	0.99 ± 0.21[c]	5.80 ± 0.60
	Overall time on damaged leaf (min)	1.18 ± 0.25[c]	6.49 ± 0.49
	Preferred site of first landing	Downwind	
	Comparison of "first evaluation" between arrangements	Recent *P. rapae* ns recent *P. xylostella* ns	

TABLE 1. CONTINUED

Comparison		Downwind plant	Upwind plant
B. Damage by different herbivores			
Recent *P. rapae* vs. fresh snail	I. Plant arrangement	Recent *P. rapae*	Fresh snail
	First landing (no.)	14	1
	Duration of first evaluation (min)	7.56 ± 0.65[c]	0.55 ± 0.37
	Overall time on damaged leaf (min)	7.80 ± 0.50[c]	0.56 ± 0.37
	II. Plant arrangement	Fresh snail	Recent *P. rapae*
	First landing (no.)	5	10
	Duration of first evaluation (min)	0.57 ± 0.27[c]	7.34 ± 0.43
	Overall time on damaged leaf (min)	0.60 ± 0.29[c]	7.34 ± 0.43
	Preferred site of first landing	Recent *P. rapae*	
	Comparison of "first evaluation" between arrangements	Recent *P. rapae* ns Fresh snail ns	
Recent *P. xylostella* vs. fresh snail	I. Plant arrangement	Recent *P. xylostella*	Fresh snail
	First landing (no.)	15	0
	Duration of first evaluation (min)	4.18 ± 0.66[c]	1.37 ± 0.37
	Overall time on damaged leaf (min)	4.71 ± 0.66[c]	1.72 ± 0.39
	II. Plant arrangement	Fresh snail	Recent *P. xylostella*
	First landing (no.)	9	6
	Duration of first evaluation (min)	0.88 ± 0.26[c]	3.28 ± 0.56
	Overall time on damaged leaf (min)	0.95 ± 0.26[c]	4.45 ± 0.52
	Preferred site of first landing	Recent *P. xylostella*	
	Comparison of "first evaluation" between arrangements	Recent *P. xylostella* ns Fresh snail ns	
C. Old vs. fresh or recent damage			
Fresh mechanical vs. old mechanical	I. Plant arrangement	Fresh mechanical	Old mechanical
	First landing (no.)	12	3
	Duration of first evaluation (min)	1.07 ± 0.20 ns	2.27 ± 0.61
	Overall time on damaged leaf (min)	3.50 ± 0.61 ns	2.27 ± 0.61
	II. Plant arrangement	Old mechanical	Fresh mechanical
	First landing (no.)	11	4
	Duration of first evaluation (min)	2.85 ± 0.53[c]	0.65 ± 0.22
	Overall time on damaged leaf (min)	3.05 ± 0.65 ns	2.68 ± 0.53
	Preferred site of first landing	Downwind	
	Comparison of "first evaluation" between arrangements	Fresh mechanical ns Old mechanical ns	

TABLE 1. CONTINUED

Comparison			Downwind plant	Upwind plant
C. Old vs. fresh or recent damage				
Recent *P. rapae* vs. old *P. rapae*	I.	Plant arrangement	Recent *P. rapae*	Old *P. rapae*
		First landing (no.)	15	0
		Duration of first evaluation (min)	6.77 ± 0.27[c]	0.06 ± 0.04
		Overall time on damaged leaf (min)	7.02 ± 0.23[c]	0.11 ± 0.08
	II.	Plant arrangement	Old *P. rapae*	Recent *P. rapae*
		First landing (no.)	9	6
		Duration of first evaluation (min)	1.93 ± 0.43[c]	3.92 ± 0.59
		Overall time on damaged leaf (min)	2.66 ± 0.62[c]	4.47 ± 0.65
		Preferred site of first landing	Recent *P. rapae*	
		Comparison of "first evaluation" between arrangements	Recent *P. rapae*[c] Old *P. rapae*[c]	
Fresh mechanical vs. old *P. rapae*	I.	Plant arrangement	Fresh mechanical	Old *P. rapae*
		First landing (no.)	15	0
		Duration of first evaluation (min)	2.12 ± 0.52 ns	1.99 ± 0.58
		Overall time on damaged leaf (min)	2.44 ± 0.39[c]	4.73 ± 0.28
	II.	Plant arrangement	Old *P. rapae*	Fresh mechanical
		First landing (no.)	15	0
		Duration of first evaluation (min)	2.20 ± 0.53 ns	2.62 ± 0.51
		Overall time on damaged leaf (min)	5.43 ± 0.36[c]	1.07 ± 0.39
		Preferred site of first landing	Downwind	
		Comparison of "first evaluation" between arrangements	Fresh mechanical ns Old *P. rapae* ns	
D. Mechanically damaged cabbage vs. mechanically damaged bean				
Fresh mechanical vs. fresh bean	I.	Plant arrangement	Fresh mechanical	Fresh bean
		First landing (no.)	13	0
		Duration of first evaluation (min)	1.37 ± 0.62 ns	0.19 ± 0.14
		Overall time on damaged leaf (min)	1.58 ± 0.66 ns	0.38 ± 0.33
	II.	Plant arrangement	Fresh bean	Fresh mechanical
		First landing (no.)	12	0
		Duration of first evaluation (min)	0.58 ± 0.29 ns	0.59 ± 0.28
		Overall time on damaged leaf (min)	0.58 ± 0.29 ns	0.59 ± 0.28
		Preferred site of first landing	Downwind	
		Comparison of "first evaluation" between arrangements	Fresh mechanical ns Fresh bean ns	

[a]Observation period 10 min. $N = 15$/arrangement.
[b]Mean ± standard error.
[c]Significant difference ($P < 0.05$).

a recently damaged cabbage (without lepidopterans) for 15 hr at 25°C before it was used in the test.

Statistical Analysis. Within and between the arrangements, the total time spent searching on each damaged leaf was compared using paired and unpaired *t* tests, respectively. To decide which plant was the preferred site of first landing, the observed choices for first landing in the two arrangements of every choice test were compiled in a 2 × 2 contingency table and compared using χ^2 test (expected values were 7.5).

RESULTS

Group A: Mechanically Damaged Cabbage vs. Cabbage Damaged by Herbivores. Wasps preferred to land on plants damaged by the lepidopterans over those damaged by mechanical means (Table 1, A). No preference was observed when mechanically damaged cabbages were in a choice test with cabbages damaged by snails or by mechanical means. When cabbage damaged by the lepidopterans was paired with mechanically damaged cabbage, wasps searched longer on the damage caused by lepidopterans both during the first evaluation and overall. When mechanical damage was paired with mechanical damage or damage caused by snails, the time spent searching was equally distributed between the two damaged leaves.

Group B: Damage by Different Herbivores. Damage produced by the lepidopterans was preferred over that produced by snails (Table 1, B). No preference was observed between cabbage damaged by *P. rapae* and *P. xylostella.* Wasps spent longer times on leaves damaged by the lepidopterans than by snails, and when only damage by the lepidopterans was present, they spent more time on leaves damaged by *P. rapae.*

Group C: Old vs. Recent or Fresh Damage. Recent damage by *P. rapae* was preferred over old, but this was not the case for fresh mechanical damage vs. old mechanical damage or old damage caused by *P. rapae* (Table 1, C). Females stayed longer on recent damage of *P. rapae* than on old, and longer on old *P. rapae* than mechanical damage, but did not treat old and fresh mechanical damage differently.

Group D: Mechanically Damaged Cabbage vs. Mechanically Damaged Bean. No preference was observed for first landing, in both arrangements, and the females spent equal amounts of time on both damaged leaves (Table 1, D).

To understand better the results of these experiments, the treated plants were divided into three categories according to the preference for landing and the time spent searching on the damaged leaves. The first category includes those plants that, although located in the upwind position, were emitting a distinctive blend of volatile chemicals that stimulated the female to fly past the downwind plant and land on the upwind one. The females spent more time on these plants. Such plants were, in group A: recently damaged by *P. rapae* (arrangement Fresh Mechanical—Recent *P. rapae*; Table 1) and recently damaged by *P. xylostella* (arrangement Fresh Mechanical—Recent *P. xylostella*); in group B: recently damaged by *P. rapae* (arrangement Fresh Snail—Recent *P. rapae*) and recently damaged by *P. xylostella* (arrangement Fresh Snail—Recent *P. xylostella*); and in group C: recently damaged by *P. rapae* (arrangement Old *P. rapae*—Recent *P. rapae*). The second category includes plants which, when in the upwind position in the arrangement, did not emit a distinctive blend of volatiles that directed the flying female over the downwind plant; the female landed on the first plant to be encountered, and the time spent on the damaged leaves of the two plants was equally distributed. Such plants are, in group A: freshly damaged by snails (arrangement Fresh Mechanical—Fresh Snail); in group D: fresh mechanically damaged bean (arrangement Fresh Mechanical—Fresh Bean); and in group C: fresh mechanically damaged cabbage (arrangement Old Mechanical—Fresh Mechanical), and old mechanically damaged cabbage (arrangement Fresh Mechanical—Old Mechanical). The third category is similar to the second category, the only difference being that the females spent longer times on one of the plants, although no preference in the first landing was observed. Such plants were, in group B: recently damaged by *P. rapae* (arrangement Recent *P. xylostella*—Recent *P. rapae*); and in group C: old damaged by *P. rapae* (arrangement Fresh Mechanical—Old *P. rapae*). Using the above divisions, the following hierarchy from most preferred to least preferred choice for first landing on damaged cabbage plants can be listed: (*P. rapae* $\cong$ *P. xylostella*) $>$ (snail $\cong$ mechanical $\cong$ bean), and recent *P. rapae* $>$ (old *P. rapae* $\cong$ fresh mechanical $\cong$ old mechanical). The hierarchy for time spent searching on damaged cabbage plants starting with the longest is *P. rapae* $>$ *P. xylostella* $>$ (snail $\cong$ mechanical $\cong$ bean).

DISCUSSION

The present study showed that the type of damage inflicted on the cabbage plants influenced the landing and the searching behavior of *C. rubecula*.

Preference for Landing. During all tests reported here the landing sites of the flying females were the damaged leaves, as was also observed in our previous study (Agelopoulos and Keller, 1994). Proof that the decision for landing is mainly governed by plant volatile chemicals related to damage is also apparent in the ability of *C. rubecula* to discriminate between plants based on the type of damage. *C. rubecula* preferred cabbages damaged by the two lepidopterans over those damaged by snails or mechanical means. The parasitoids *Cotesia glomerata* and *C. marginiventris* responded similarly when host-plants damaged by their hosts were paired with host-plants damaged by mechanical means (Turlings et al., 1990; Steinberg et al., 1993). Although the above-mentioned preference for damaged plants by the lepidopterans over those damaged by snails or mechanical means showed that the volatile blends emitted were different, at this stage we cannot attribute the difference to the type of damage. Mechanical damage and damage caused by snails were inflicted on the plant just before the commencement of the tests, in comparison to damage by the lepidopterans, which was produced over a period of 24 hr. Further investigation is needed to understand if continuity of damage for a period of 24 hr induces the plant to produce a volatile blend different from that produced by short-term damage. *C. rubecula* could not distinguish while flying between cabbages damaged by *P. rapae* and cabbages damaged by *P. xylostella*. This can be attributed to the experience of females or to the fact that feeding by *P. rapae* induces the plant to produce more or less the same volatile chemicals as feeding by *P. xylostella*. We have to take into consideration that the females used for the tests had not been exposed to host-infested plants for 24 hr. Females of the parasitoid *Microplitis croceipes*, which had a preflight experience just before the commencement of the test with a cowpea-*Heliothis zea* complex, expressed a stronger attraction to *H. zea* than to *Spodoptera frugiperda* (nonhost species) feeding on cowpea (Zanen and Cardé, 1991). Further investigation is needed to understand if exposure of females to a host-infested plant just before the commencement of the experiment can affect their ability to distinguish between cabbages damaged by the two lepidopterans. Finally, *C. rubecula* favored recent over old damage caused by its host, indicating that when damage by larvae has stopped, the plant does not release the same volatile chemicals as when currently damaged by larvae.

Searching Behavior on Damaged Leaves. Both the time of first evaluation and the overall time spent searching on the damaged leaves was influenced by the type of damage. Damage caused by the lepidopterans was searched more intensively than damage caused by snails or mechanical means. When plants damaged by the lepidopterans were tested together, the females searched considerably longer on the leaf damaged by the host, implying that the two lepidopterans left different stimuli on the damaged leaves. The complexity of factors involved in searching behavior once a female is on a plant should not be underestimated. The stimuli encountered on a damaged leaf could be chemicals originating from the host or the plant. When there was a total absence of chemicals by the lepidopterans on plants, as in the case of mechanically damaged cabbage and beans, the females palpated the undamaged and damaged sites of the leaves, indicating that searching was induced by plant chemicals. The involvement of chemicals originating from the larvae in our experiment needs further study, as it is unknown if removing the larvae and their by-products and washing the plant with water is sufficient to remove all the chemicals related to them. It is easy to attribute the longer searching time on leaves damaged by the host to host chemicals left on the leaves, but it is not easy to explain the fact that *C. rubecula* searched significantly longer on leaves damaged by *P. xylostella* over those damaged by mechanical means or snails. *P. xylostella* is not a host species. We suspect that the two species have some chemicals in common, as they utilize a similar range of host plants. It has been shown that frass of Lepidoptera feeding on the same host plant contains some common chemicals (Thibout et al., 1993), and it may be that this is a case of contamination by common frass chemicals. One could argue that *P. xylostella* has completely different kairomones from *P. rapae* but because infestations of both species commonly occur on the same plant, *C. rubecula* uses the kairomones of *P. xylostella* as indicators of the presence of its host nearby. We think this is unlikely, as kairomones of *P. xylostella* would not be reliable where infestation of *P. xylostella* occurs separately from that of *P. rapae* (Vet et al., 1991).

Movements between Plants. In all arrangements, both plants were visited by several wasps, and, in most cases, the downwind plant was the first to be searched. It seems that the decision to leave the downwind plant and fly to the upwind plant was induced by the absence of the host and, at the same time, by the perception of chemicals related to damage of a cabbage nearby (upwind plant). The upwind plant was searched as well. There were many cases where, after searching the upwind plant, the female wasps drifted back to the downwind plant. It seems that the decision to leave the upwind plant was induced by the absence of the host and the absence in the air of volatile chemicals related to damage. Memory of what had been encountered previously may be one of the factors involved in making the decision to fly back. The nonhost plant species, bean, was also visited and searched, implying that *C. rubecula* may spend time on damaged nonhost plant species during its search for hosts if nothing more attractive is near.

From the results of this and our previous study, we conclude that the plant is a substantial source of information to searching females of *C. rubecula*. It provides information about the presence and location of damage; if the damage is caused by Lepidoptera, other herbivores, or mechanical means; and if it is recent or old in the case of damage caused by Lepidoptera. The parasitoid species *Cotesia marginiventris* (Cresson) and *Cotesia glomerata* L. utilize the information emitted by their host-plants in a similar way (Steinberg et al., 1993; Turlings et al., 1990, 1991).

Identification of the volatile chemicals released by cabbage is needed to determine how the damage produced by various means and the duration of damage affect the volatile blend released.

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