*Journal of Chemical Ecology, Vol. 22, No. 2, 1996*

# VOLATILE INFOCHEMICALS USED IN HOST AND HOST HABITAT LOCATION BY *Cotesia flavipes* CAMERON AND *Cotesia sesamiae* (CAMERON) (HYMENOPTERA: BRACONIDAE), LARVAL PARASITOIDS OF STEMBORERS ON GRAMINAE

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(Received March 20, 1995; accepted October 15, 1995)

**Abstract**—Female *Cotesia flavipes* Cameron and *Cotesia sesamiae* (Cameron) were attracted to odors in a Y-tube olfactometer from uninfested maize (*Zea mays* L.), sorghum [*Sorghum bicolor* (L.)], and napier grass (*Pennisetum purpureum* Schumach). In dual choice tests, *Cotesia flavipes* showed a preference for maize over sorghum, while maize and napier grass were equally attractive. In contrast, *Cotesia sesamiae* preferred volatiles from sorghum and napier grass over those from maize. The two parasitoids were significantly more attracted to maize infested with the stemborers, *Chilo partellus* (Swinhoe), *Chilo orichalcociliellus* Strand, *Sesamia calamistis* Hampson, and *Busseola fusca* (Fuller), than uninfested maize. In dual choice tests, *Cotesia flavipes* and *Cotesia sesamiae* were unable to discriminate between odors from plants infested by the different species of stemborers.

**Key Words**—Host location, host habitat location, *Cotesia flavipes, Cotesia sesamiae*, Hymenoptera, Braconidae, cereals, parasitoid, stemborers, Lepidoptera, Pyralidae, Noctuidae, Y-tube olfactometer.

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## INTRODUCTION

Classical biological control has been used as a strategy for suppressing populations of introduced lepidopteran pests in the tropics. The success of classical biological agents has been attributed in part to the high searching efficiency of the natural enemy for its host (Waage, 1990). The ability of a natural enemy to locate a suitable host in a complex environment is critical to its successful establishment in a new environment (Nordlund et al., 1988). The host selection process is divided into three steps: host habitat location, host location, and host acceptance (Vinson, 1976). Allelochemicals are known to play an important role in this process. Chemicals emitted by plants influence the searching behavior of parasitoids (Nordlund et al., 1988; Lewis and Martin, 1990; Vet and Dicke, 1992; Dicke, 1994; Godfray, 1994). In addition, females of many insect parasitoids may rely on host and host-related chemicals (e.g., from frass) in their search for hosts (Vinson, 1976; Weseloh, 1981; Arthur, 1981; Vet and Dicke, 1992). However, host-produced chemicals often play a much less important role in long-distance searching by parasitoids than do plant-produced chemicals (Turlings et al., 1991a,b; Vet and Dicket, 1992; Steinberg et al., 1993; Geervliet et al., 1994; Potting et al., 1995a).

*Chilo partellus* (Swinhoe) (Pyralidae) is one of the major lepidopterous stemborer pests of cereal crops in Kenya (Overholt et al., 1994a). This pest was introduced into Africa sometime in the early 1930s (Tams, 1932). Indigenous natural enemies, including the larval parasitoid, *Cotesia sesamiae* (Cameron), are not able to maintain the pest population density at a level acceptable to farmers (Oloo, 1989; Overholt et al., 1994a). *Cotesia flavipes* Cameron, which has been used successfully in classical biological control of gramineous stemborers in other parts of the world (Overholt et al., 1994b), was introduced into Kenya from Pakistan in an attempt to reduce the severity of the stemborer problem.

*Chilo partellus* is found in cultivated gramineous plants together with indigenous stemborer species, which include *Chilo orichalcociliellus* Strand (Pyralidae), *Busseola fusca* (Fuller), and *Sesamia calamistis* Hampson (Noctuidae). The same complex of stemborer species is also found on wild grasses (Mathez, 1972; Seshu Reddy, 1989; Harris, 1990). Little is known about the foraging behavior of *Cotesia flavipes* and *Cotesia sesamiae* in the system comprising the stemborers and plants mentioned above. It was reported that *Cotesia flavipes* cannot discriminate between maize infested with *Chilo partellus* and maize infested with *B. fusca* (Potting et al., 1993). However, *Cotesia flavipes* showed a preference for maize stems with feeding *Chilo partellus* larvae over artificially damaged maize, larvae alone, host frass, or uninfested maize (Potting et al. 1995a). It is not known whether this parasitoid is attracted to the different gramineous plants (which are the food of its hosts, e.g., maize, sorghum, napier grass) occurring in the area of release, the coast of Kenya. It is also not known whether *Cotesia flavipes* has a preference for any of these host plants either uninfested or infested by larvae of different stemborer species (*Chilo orichalcociliellus, Chilo partellus, S. calamistis*) occurring in that area. No information is available on the host selection process of the closely related indigenous parasitoid, *Cotesia sesamiae*. The extent of overlap in the niches of the two *Cotesia* species also is not known. The aim of this study was, therefore, to investigate the response of *Cotesia flavipes* and *Cotesia sesamiae* to volatiles from uninfested maize, sorghum and napier grass and the response of both parasitoids to volatiles from different stemborer–plant complexes that are likely to be found in the area of release.

## METHODS AND MATERIALS

### *Parasitoids*

A colony of *Cotesia flavipes* was started in 1991 from material collected from *Chilo partellus* at Rawalpindi, Pakistan, by the International Institute of Biological Control (IIBC). The *Cotesia sesamiae* colony was also started in 1991 with material collected from *Chilo partellus* in the coastal zone of Kenya. *Cotesia flavipes* and *Cotesia sesamiae* were reared on *Chilo partellus* and *S. calamistis* larvae, respectively, according to the method described by Overholt (1993). *Chilo partellus* and *S. calamistis* are among the respective natural hosts of *Cotesia flavipes* and *Cotesia sesamiae*. After parasitization, stemborers were maintained on artificial diet (Ochieng et al., 1985; Onyango and Ochieng'-Odero, 1994) at 25°C, 65–70% relative humidity, and 12L:12D photoperiod. Parasitoid cocoons were collected in glass vials and kept in a clean Perspex cage until emergence of adults. Adult parasitoids were provided a 20% honey-water solution as diet. One-day-old, mated, naive female parasitoids were used in all experiments.

### *Stemborers*

*Chilo partellus, S. calamistis*, and *Chilo orichalcociliellus* were collected from maize fields near the Kenyan coast. A colony of *B. fusca* was initiated with larvae and pupae collected from maize in western Kenya. Larvae of *Chilo* spp. were reared on an artificial diet developed by Ochieng et al. (1985). The noctuids, *B. fusca* and *S. calamistis*, were reared on media described by Onyango and Ochieng'-Odero (1994). Prior to any experiment, stemborer larvae were removed from artificial diet and fed on fresh maize stems for 48 hr.

### *Plants*

Maize (*Zea mays* L., hybrid 5-11) and sorghum [*Sorghum bicolor* (L.), Serena cultivar], were grown in 20-liter plastic buckets in a nursery at the International Centre of Insect Physiology and Ecology (ICIPE). Potted plants were kept under large field cages (2 × 2 × 2 m), which were covered with fine mesh (400 $\mu$m) netting to protect them from insect attack. Additional maize plants were grown in the field. Napier grass (*Pennisetum purpureum* Schumach.) was collected from farmers' fields near Nairobi.

### *Behavior Assays*

The Y-tube olfactometer used in this study has been described by Steinberg et al. (1992). The odor sources were placed in two Perspex chambers (30 × 30 × 120 cm) sufficiently large to accommodate whole plants (2–3 months old) (Figure 1). One of the square ends of the chamber was left open. For the system

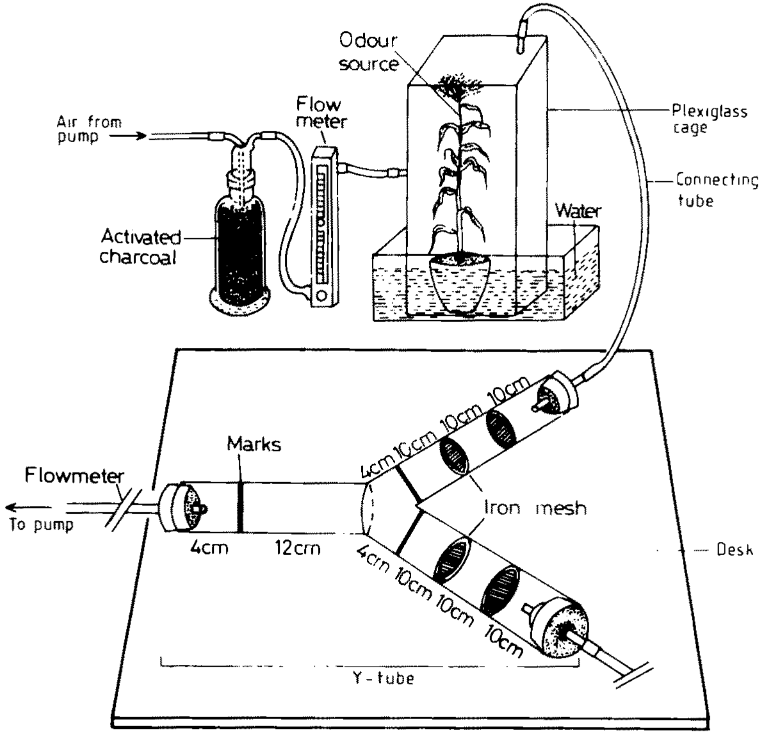

FIG. 1. A schematic diagram of the Y-tube olfactometer.

to be airtight, the open end of each box was placed over the test material, which stood in water held in a plastic basin. The open end was submerged 15 cm below the meniscus. The two chambers were connected to the arms of the Y-tube with Tygon tubing from the top of the chambers. An inlet, through which clean air entered the chamber, was drilled 30 cm from the bottom of the chamber on one side. One vacuum pump (Cole-Parmer Air-Cadet) drew and pushed air through the closed system. Air was pushed through an activated charcoal filter into the two chambers and drawn into the Y-shaped glass tubing of the olfactometer. The airflow was set at 2.5 liters/min for each arm. Parasitoids were released individually in the stem of the Y-tube and allowed 5 min to choose one of the arms. When a parasitoid remained more than 15 sec beyond the finishing line (4 cm past the intersection), it was recorded as a choice. The connections of the odor source chambers to the arms of the olfactometer were reversed after testing five insects to rule out the effect of asymmetrical bias in the olfactometer or its surroundings. A cream-white curtain was used to separate the experimental area from the surroundings. Tests were conducted at 23–26°C, 65–75% relative humidity, and light intensity of 350–450 lux. All tests were replicated at least three times with 20 parasitoids per replicate. Data were analyzed using the log likelihood ratio test (*G* test) for goodness of fit (Sokal and Rohif, 1981).

*Response to Volatiles from Uninfested Plants.* Uninfested maize, sorghum, and napier grass plants 8–10 weeks old were used in the experiments. All plant species were tested in single and dual choice experiments in the Y-tube olfactometer.

A first series of experiments was conducted to determine the attractiveness of odors from uninfested plants. Maize, napier grass, and sorghum were tested in single choice experiments. Individual parasitoids were given a choice between odor from potted maize and air drawn over a pot with soil only, odors from potted sorghum plant and air drawn over a pot with soil only, and finally odor from napier grass cut above the soil level and air drawn over an empty chamber.

A second series of tests was conducted to determine the parasitoid's preference for odors from different uninfested plant species. Plants were placed in chambers connected to both arms of the olfactometer. An approximately similar biomass of plants was used for each arm. Attractiveness of volatiles from potted maize was compared with attractiveness of volatiles from potted sorghum, and odors from maize plants from the field excised above soil level were compared with that of napier grass treated the same way. Field materials were checked for damage before each test and dissected after a test to establish it was uninfested.

*Response to Volatiles from Plants Infested by Different Stemborer Species.* In the Y-tube olfactometer, parasitoids were given a choice between odors from plants infested with different stemborer species [plant–herbivore complex (PHC)] and uninfested plants. The following PHC combinations were tested against the control (uninfested plants): (1) maize plants infested with *Chilo partellus*, (2) maize plants infested with *Chilo orichalcociliellus*, and (3) maize plants infested with *S. calamistis*. Potted maize plants were infested with two fourth instars by boring two holes in the maize stem (1 cm deep) with a 4-mm cork borer and placing one larva in each hole. Larvae were allowed to feed overnight, and tests were conducted 18–20 hr after infestation. Holes were also made in control plants, but no larvae were introduced. Plants were transferred into the chambers connected to the Y-tube in the pot in which they were grown 30 min before observations were made (to allow time for volatiles to be released in the chamber). Only plants grown in pots were used in this test. In a few cases potted plants that were too tall to enter the test chamber were excised and tested. Plants in both arms were treated in the same manner (cut at the base or kept in pots).

A second series of tests was conducted to determine the parasitoids' preference between plants infested by different stemborer species. The following combinations were tested: (1) maize infested with *Chilo partellus* larvae versus maize infested into *Chilo orichalocociliellus* larvae, (2) maize infested with *Chilo partellus* larvae versus maize infested with *S. calamistis* larvae, and (3) maize infested with *Chilo partellus* larvae versus maize infested with *B. fusca* larvae [only *Cotesia sesamiae* was used for the test with *B. fusca; Cotesia flavipes*' response having already been studied by Potting et al. (1993)].

A third series of tests was conducted to determine the response of parasitoids depending on the number of stemborer larvae feeding of the plant. The following number/species combinations of stemborers per plant were compared: (1) two *Chilo partellus* versus 10 *S. calamistis*, (2) five *Chilo partellus* versus five *S. calamistis*, (3) 10 *Chilo partellus* versus two *S. calamistis*, and (4) two *B. fusca* versus ten *Chilo partellus* larvae.

## RESULTS

*Response to Volatiles from Uninfested Plants. Cotesia flavipes* and *Cotesia sesamiae* were more attracted to odors from gramineous plants (maize, sorghum, napier grass), the habitat of their host, than to the control, clean air (Figure 2). *Cotesia flavipes* did not exhibit a preference between maize and napier grass (Figure 3). However, maize was preferred over sorghum by *Cotesia flavipes*, whereas *Cotesia sesamiae* preferred sorghum over maize (Figure 3). The preferences of the two parasitoids significantly differed (contingency table, $\chi^2 = 16.71$, $df = 1$; $p < 0.001$); *Cotesia sesamiae* also preferred napier grass over maize (Figure 3).

*Response to Maize Plants Infested by Different Stemborer Species.* Parasitoids of both species preferred odors from maize plants infested with two larvae

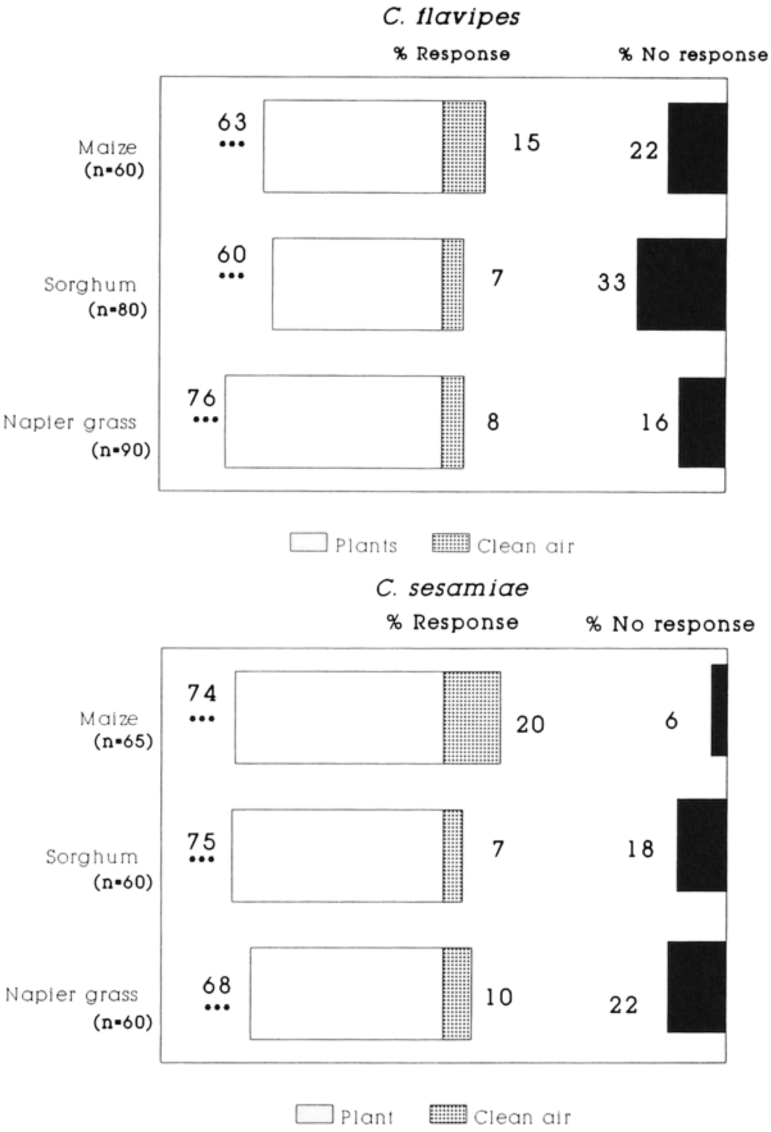

FIG. 2. Response of naive *Cotesia flavipes* and *Cotesia sesamiae* to odors from uninfested plants versus clean air in a Y-tube olfactometer. $N$ = number of replicates. Numbers next to the bars indicate the percentages of parasitoids that made a choice for one of the two odor sources or did not make a choice at all. The three percentages add up to 100%. Asterisks indicate significant differences within the choice test: $*P < 0.05$, $**P < 0.01$; $***P < 0.001$, ns = not significant, $G$-test for goodness of fit.

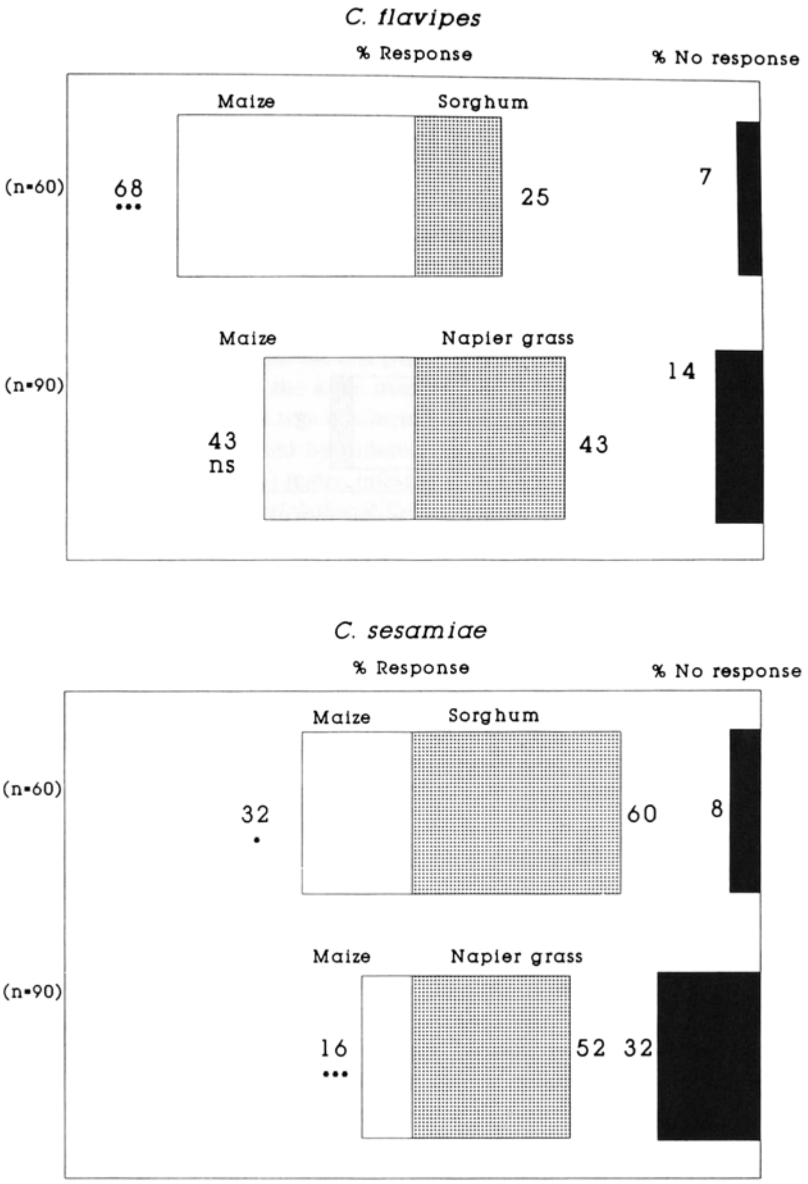

FIG. 3. Response of naive *Cotesia flavipes* and *Cotesia sesamiae* to odors from uninfested plants in two-choice tests in the Y-tube olfactometer. For other explanations see legend of Figure 1.

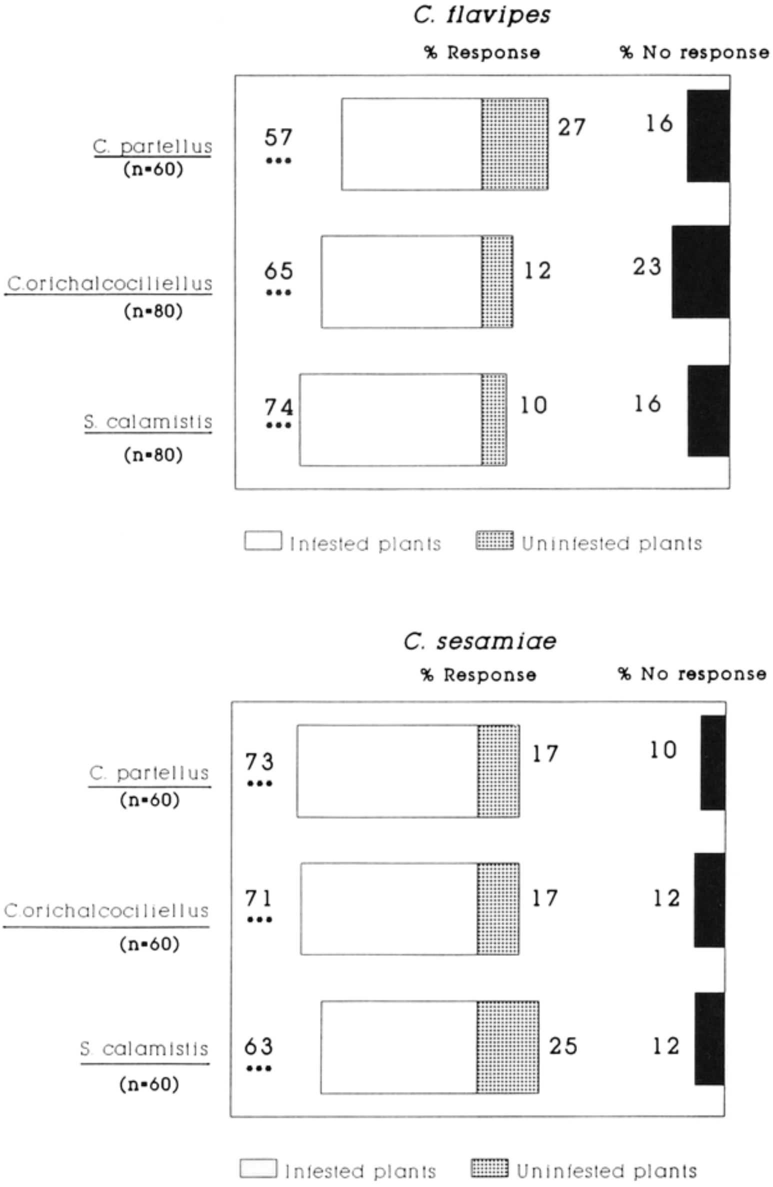

FIG. 4. Response of naive *Cotesia flavipes* and *Cotesia sesamiae* to odors from maize plants infested with different stemborer species versus uninfested maize plants in a Y-tube olfactometer. For other explanations see legend of Figure 1.

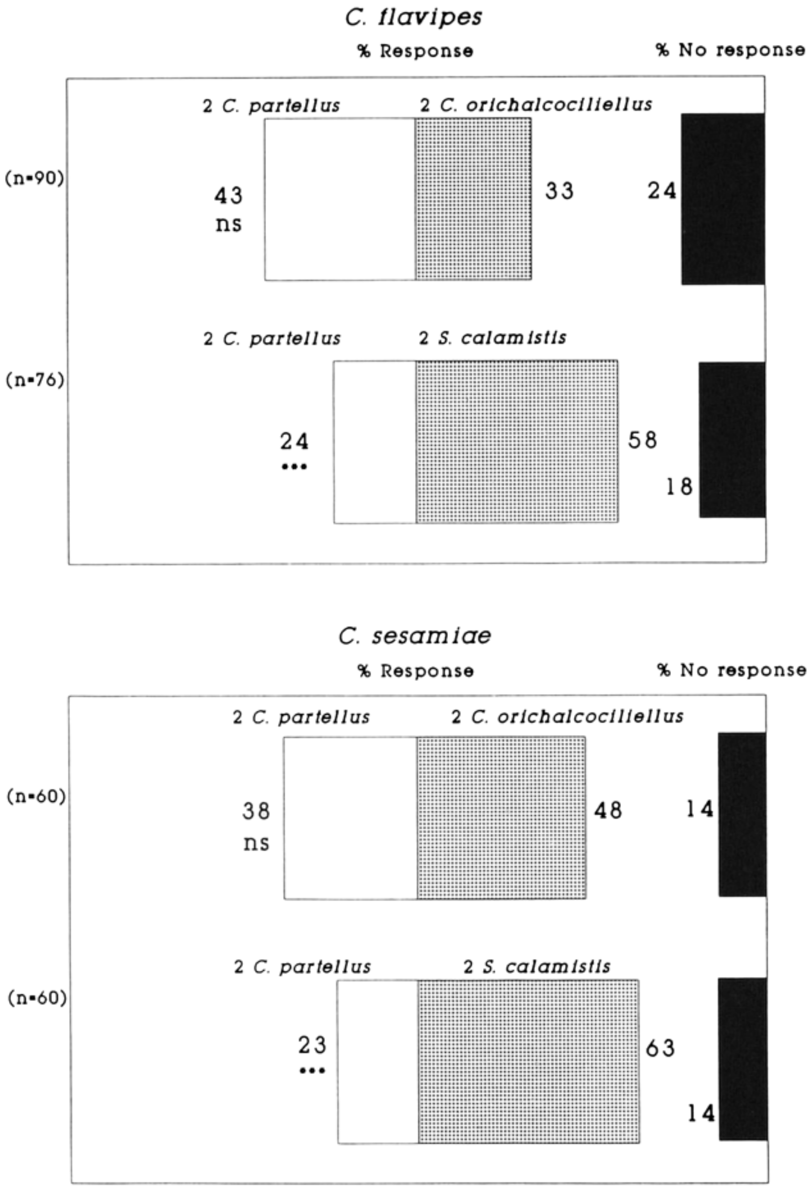

FIG. 5. Response of naive *Cotesia flavipes* and *Cotesia sesamiae* in the Y-tube olfactometer to odors from maize plants infested with two stemborer larvae per plant, in two-choice tests. For other explanations see legend of Figure 1.

of *Chilo partellus*, *S. calamistis*, or *Chilo orichalcociliellus*, per plant, over odors from uninfested maize plants (Figure 4).

When maize plants infested with two larvae of one of two species were offered in dual choice situations, both parasitoid species preferred odors of plants infested by *S. calamistis* over those infested with *Chilo partellus*. Neither parasitoid species discriminated between maize plants infested with two *Chilo partellus* larvae and maize plants infested with two *Chilo orichalcociliellus* larvae (Figure 5).

Several other combinations were tested with *Chilo partellus* and *S. calamistis* as herbivores. When maize plants infested by two larvae of one species were offered versus plants infested by 10 larvae of the other, *Cotesia flavipes* preferred odors from maize plants infested with 10 larvae in both cases. When odors from plants infested with five *Chilo partellus* larvae were offered versus odors from plants infested with five *S. calamistis* larvae, *Cotesia flavipes* females did not discriminate (Figure 6).

*Cotesia sesamiae* preferred odors from maize plants infested with two larvae of *B. fusca* over odors from uninfested maize. This parasitoid also preferred

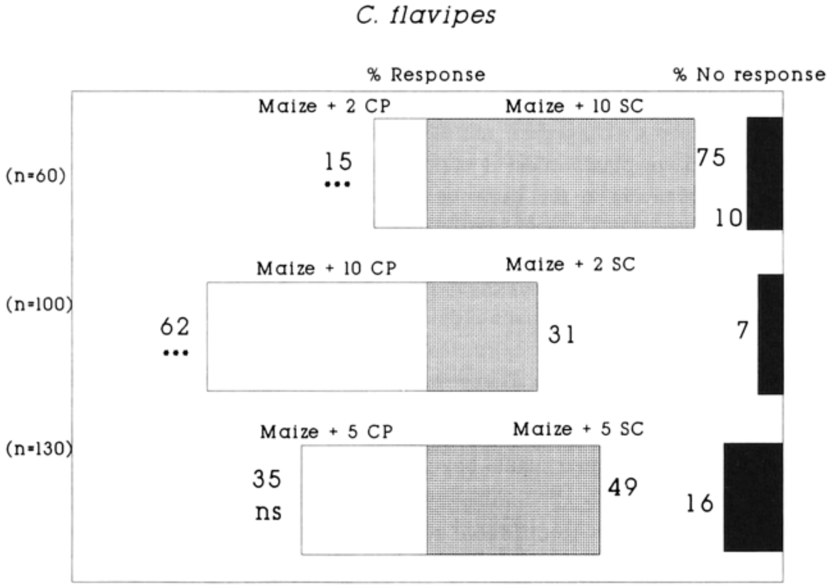

FIG. 6. Response of naive Cotesia flavipes in the Y-tube olfactometer to odors from maize plants infested with larvae of *Chilo partellus* (CP) or *Sesamia calamistis* (SC) at different densities. For othr explanations see legend of Figure 1.

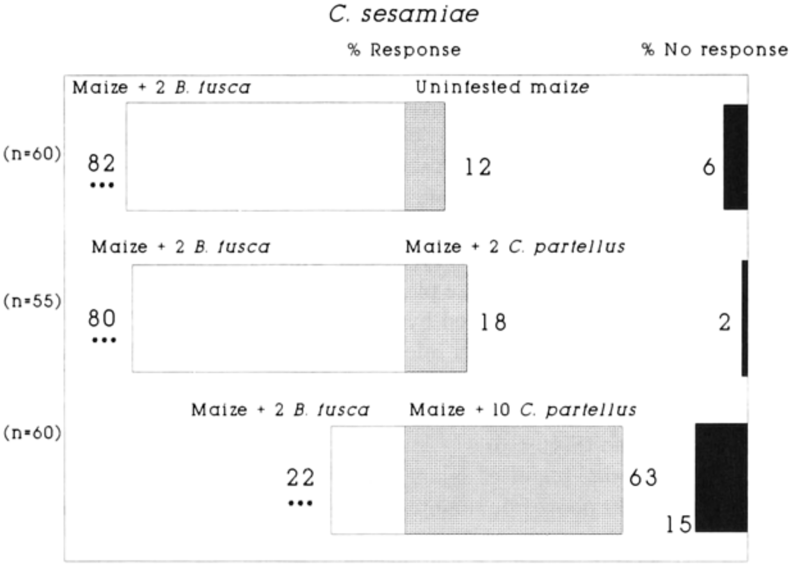

FIG. 7. Response by naive *Cotesia sesamiae* in the Y-tube olfactometer to odors from uninfested maize plants and maize plants infested with larvae of *B. fusca* and plants infested with larvae of *Chilo partellus* or *B. fusca* at different densities. For other explanations see legend of Figure 1.

odors from maize plants infested with *B. fusca* over odors from those infested with *Chilo partellus* at the same density (two larvae per plant) (Figure 7). However, when plants where infested with 10 *Chilo partellus* larvae and two *B. fusca* larvae, *Cotesia sesamiae* showed preference for odors emanating from plant infested with *Chilo partellus* (Figure 7).

## DISCUSSION

Plant odors play an important role in communication in tritrophic systems. Volatiles from uninfested plants have been found to be long-range attractants for parasitoids (Vinson, 1985; Nordlund et al., 1988; Whitman, 1988; Williams et al., 1988; Lewis et al., 1990). For example, *Campoletis sonorensis* (Cameron) is attracted to uninfested food plants of its hosts (Elzen et al., 1983). *Macrocentrus grandii* Goidanich, a larval parasitoid of the European corn borer, *Ostrinia nubilalis* (Hübner), is also attracted to several plant species including its host's food, uninfested maize (Ding et al., 1989). In the present study, *Cotesia flavipes* and *Cotesia sesamiae* were strongly attracted to odors emanating from several gramineous plants (maize, sorghum, and a wild host, napier grass), which are host plants of stemborers. In all single-choice tests, the gramineous plant was selected over the control, regardless of the plant species. *Cotesia flavipes* showed a preference for maize over sorghum in the dual choice experiments. This parasitoid was imported from Pakistan, where it was collected from *Chilo partellus* in maize fields. This preference may, therefore, be a reflection of a genetic adaptation to searching in maize. In contrast, the indigenous parasitoid *Cotesia sesamiae* was more attracted to sorghum odors, and this may have been due to a genetic adaptation as well: there has been a long history shared by *Cotesia sesamiae* and sorghum, which has its center of origin in Africa (Doggett, 1988). Except for a few records showing *Cotesia flavipes* attacking *Diacrisia obliqua* Walker and *Porthesia scintillans* Walker, feeding on castor in India (Muthukrishnan and Senthamizhselvan, 1987; Senthamizhselvan and Muthukrishnan, 1989), *Cotesia flavipes* and *Cotesia sesamiae* have been collected only from noctuid and pyralid hosts feeding on gramineous plants (Polaszek and Walker, 1991). This specificity suggests that plants provide important cues to the searching parasitoids. Similarly, it was reported that taxonomically unrelated hosts feeding on the same species of plants frequently shared the same parasitoids (Picard and Rabaud, 1914) and that the amount of parasitism suffered by a polyphagous host species may often depend on the food plant attacked (Vinson, 1981, 1985; Nordlund et al., 1988).

*Cotesia flavipes* and *Cotesia sesamiae* preferred odors from infested plants over odors from uninfested plants, indicating that both parasitoids were able to identify plants attacked by their hosts. Similar findings have been reported in several tritrophic systems [see Vet and Dicke (1992) for a review]. Dicke et al. (1990a,b) reported that Lima bean and cucumber plants infested with two spotted spider mites, *Tetranychus urticae* Koch, emitted a blend of volatiles that attracted the predatory mites *Phytoseiulus persimilis* Athias-Henriot. Turlings et al. (1990a,b; 1991a,b) found that maize plants damaged by the beet armyworm [*Spodoptera exigua* (Hübner)] emitted volatile chemicals that were attractive to the parasitoid *Cotesia marginiventris* (Cresson).

Odors from maize plants infested with two *S. calamistis* were more attractive to *Cotesia flavipes* and *Cotesia sesamiae* than odors from maize plants infested with a similar number of *Chilo partellus* larvae. *Sesamia calamistis* is a larger stemborer and feeds more voraciously than *Chilo partellus*, thereby inflicting greater injury to the plant and producing greater quantities of frass. The quantities of volatiles emitted may be proportional to the amount of plant injury, and that could explain the greater attraction to plants infested with *S. calamistis*. This hypothesis is supported by the fact that a larger number of hosts on a plant increased attractiveness (Figure 6). Similar observations were made when *Cotesia sesamiae* was exposed to odors from plants infested with *B. fusca*, also a large stemborer, and *Chilo partellus* (Figure 7). In a related study, Potting et al. (1993) found that odors from maize plants infested with two larvae of *B. fusca* were more attractive to *Cotesia flavipes* than odors from maize plants infested with two larvae of the smaller *Chilo partellus*. These results strongly suggest that the two parasitoids are not able to discriminate between maize plants infested by the four herbivore species under study and that they both seem to use a similar set of stimuli to locate their hosts. In contrast, *Cotesia marginiventris*, which is a generalist parasitoid of numerous species of leaf-feeding insects on a wide range of plants, is able to distinguish between odors of two different plants fed on by the same host and also between two different host species feeding on the same plant species (Turlings et al., 1989). Different herbivore species may cause a differential release of plant compounds that can be detected by parasitoids after experience (Turlings et al., 1990a). For *Cotesia flavipes*, however, learning has not been detected (Potting et al., unpublished data), possibly because the insects live for only 2–3 days (Moutia and Courtois, 1952; Gifford and Mann, 1967; Kajita and Drake, 1969; Potting et al., 1995b). Because of their short life-span, females of *Cotesia flavipes* may search primarily within the habitat where they emerge and may have adapted to attacking all lepidopterous stemborers occurring in that habitat.

*Cotesia flavipes* was released in the coastal area of Kenya in 1993. The primary target of this biological control program was the introduced stemborer *Chilo partellus*. However, two other stemborer species, *S. calamistis* and *Chilo orichalcociliellus*, occur in the same ecosystem. During the two cropping seasons (long rains, April–June; short rains, October–December), all three stemborer species coexist in maize fields (Overholt et al., 1994a) and in wild grasses (J.C. Mbapila, unpublished data). In periods between cropping seasons, some stemborers estivate in maize stubbles, while others remain actively feeding in wild grasses, including napier grass, in the proximity of cultivated areas (J.C. Mbapila, unpublished data). The results of this study suggest that *Cotesia flavipes* may be able to search and attack all three stemborer species in cultivated and wild grasses during the cropping seasons and in wild grasses during periods between cropping seasons. Moreover, when maize and sorghum are grown in proximity, our results suggest that *Cotesia flavipes* may exhibit a greater propensity for searching in maize.

Cotesia flavipes and *Cotesia sesamiae* are attracted to odors from the same host habitats, which suggests that the niches of the two parasitoids overlap and competition for hosts is likely to occur. However, due to the differences observed in host-plant preference and host suitability (Ngi-Song et al., 1995), both parasitoids may persist in the same region.

*Acknowledgments*—This work was supported by the German Academic Exchange Services (DAAD) and the Directorate General for International Cooperation, The Netherlands, under a collaborative project between The International Center of Insect Physiology and Ecology (ICIPE) and Wageningen Agricultural University entitled "Biological Control of Tsetse and Crop Pests."

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