DIFFERENTIAL ATTRACTIVENESS OF INDUCED ODORS EMITTED BY EIGHT MAIZE VARIETIES FOR THE PARASITOID *Cotesia marginiventris*: IS QUALITY OR QUANTITY IMPORTANT?

MARIA ELENA FRITZSCHE HOBALLAH, CRISTINA TAMÒ, and TED C. J. TURLINGS*

Université de Neuchâtel, Institut de Zoologie
Laboratoire d'Ecologie Animale et Entomologie (LEAE)
Case Postale 2, 2007 Neuchâtel, Switzerland

Abstract—Herbivore-induced plant volatiles can function as indirect defense signals that attract natural enemies of herbivores. Several parasitoids are known to exploit these plant-provided cues to locate their hosts. One such parasitoid is the generalist *Cotesia marginiventris*, which is, among others, attracted to maize volatiles induced by caterpillar damage. Maize plants can be induced to produce the same blend of attractive volatiles by treating them with regurgitant of *Spodoptera* species. We collected and analyzed the regurgitant-induced emissions of two plant species (cowpea and maize) and of eight Mexican maize varieties and found significant differences among their volatile emissions, both in terms of total quantity and the quality of the blends. In a Y-tube olfactometer, the odors of the same artificially induced plant species and Mexican varieties were offered in dual choice experiments to naïve mated females of *C. marginiventris*. Wasps preferred cowpea over maize odor and, in 3 of 12 combinations with the maize varieties, they showed a preference for the odors of one of the varieties. A comparison of the odor collection with results from the behavioral assays indicates that not only the quantity of the volatile emissions, but also the quality (composition) of the volatile blends is important for attraction of *C. marginiventris*. The results are discussed in the context of the possibility of breeding crop varieties that are particularly attractive to parasitoids.

Key Words—Induced plant volatiles, parasitoid, olfactometer, *Cotesia marginiventris*, *Spodoptera littoralis*, *Zea mays*, *Vigna unguiculata*, parasitoid attraction, odor variability.

* To whom correspondence should be addressed. E-mail: ted.turlings@unine.ch

INTRODUCTION

Herbivore-induced odors have been suggested to benefit plants in different ways (Vet and Dicke, 1992; Turlings and Benrey, 1998; Sabelis et al., 1999; Dicke and van Loon, 2000). Over the last 15 years, it has become evident that these odors are important for the attraction of natural enemies to the microhabitat of their prey (e.g., Dicke et al., 1990a; Turlings et al., 1990a; Steinberg et al., 1993; Du et al., 1998; Röse et al., 1998). The blend of odors released by plants after herbivore attack is variable, depending on the plant (species and variety) and the herbivore that feeds on it, although some compounds are common to many induced blends (for reviews see Dicke, 1994, 1999). It is known that European maize varieties and their wild ancestors differ considerably in quality and quantity of odors if induced to produce volatiles by treating scratched leaves with *Spodoptera littoralis* (Lepidoptera: Noctuidae) regurgitant (Gouinguené et al., 2001). We define differences in the quality of the odor blends as differences in the presence of specific compounds in the blend and/or the proportions among compounds. This variation among maize varieties could have important consequences for pest management, as biological control may be more effective for varieties that are highly attractive to natural enemies. This may be particularly true for countries in Latin America where the major pests of maize are leaf-feeding *Spodoptera* caterpillars (for review see Andrews, 1988).

Young *Spodoptera* caterpillars can be parasitized by *Cotesia marginiventris* (Hymenoptera: Braconidae), a common solitary endoparasitoid that attacks Lepidopteran larvae during the first and second instar (Jalali et al., 1987). *C. marginiventris* females are strongly attracted by the odors emitted by caterpillar-damaged maize seedlings (Turlings et al., 1990a, 1991a) and spend more time on caterpillar-damaged plants than on artificially damaged or unattacked plants (Loke et al., 1983). Maize plants infested with a *Spodoptera* larva parasitized by *C. marginiventris* produce more seeds than plants infested with a healthy caterpillar (Fritzsche Hoballah and Turlings, 2001), which could translate into a higher yield for maize cultivars that are particularly attractive to the parasitoid. Hence, it seems important to know which factors determine the attractiveness of the crop.

Here we report on how differences in induced volatile emissions among different plant genotypes may affect the attractiveness of these genotypes to parasitoids. We first compared the emissions of maize and cowpea and their attractiveness to *C. marginiventris*. The former plant species is known to release large amounts of induced volatiles (e.g., Turlings et al., 1998), while the latter releases relatively little, but can be quite attractive (Whitman and Eller, 1990). Furthermore, we investigated the attractiveness of eight Mexican maize cultivars. In Y-tube olfactometer, naïve *C. marginiventris* females were offered a choice between the odors of the two respective plant species or 12 paired combinations of the Mexican maize varieties. Comparison of the results from these behavioral assays with the

odor blends that were collected from the various plants revealed that for naïve wasps attractiveness is not simply a matter of quantity of volatiles, but that the quality of the blend is important as well.

METHODS AND MATERIALS

Growing and Treatment of Plants. Plants used in all experiments were grown in plastic pots (6 cm high, 8 cm diam.) in fertilized commercial soil (Coop) in a climate chamber (23°C, 60% relative humidity, and 16L:8D, 50,000 lumens/m^2). Two-week-old *Vigna unguiculata* (var. kpodii-guegue, obtained from IITA) Africa) and 10-day old *Zea mays* (var. Delprim and varieties obtained from CIMMYT, Table 1) plants were used for the experiments. To induce the plants to produce volatiles, we scratched two leaves (the second and third leaf of maize and first and second of cowpea) of each plant with a razor blade (an area of 2–4 cm^2/leaf) and subsequently applied on each damaged site 10 μl of regurgitant. Regurgitant was collected from fourth and fifth instar *S. littoralis* caterpillars (for the method, see Turlings et al., 1993a) and kept at −70°C until just before utilization. After treatment, plants were placed for 5 hr (plant species) and 6 hr (varieties), under three fluorescent lamps (Sylvania standard F36W 133-T8 cool white, 5000 lumens/m^2 at pot height), before they were used for the volatile collection and olfactometer experiments. It is known that 5–6 hr after treatment corn plants emit relatively large quantities of induced volatiles (Turlings et al., 1998).

Insects. *S. littoralis* caterpillars and eggs were supplied weekly by Syngenta (Stein, Switzerland). Eggs were incubated in Petri dishes (9 cm diam., 1.5 cm high) on moist filter paper. Emerged caterpillars were fed with artificial diet and kept in plastic-boxes (15 × 9 × 5 cm) under ambient laboratory conditions. This non-native host causes a similar reaction in plants as the natural host *S. frugiperda* (Fritzsche Hoballah, unpublished data).

TABLE 1. VARIETY NUMBER, NAME, ORIGIN, AND SEED COLOR OF 8 MEXICAN CORN VARIETIES USED FOR VOLATILE COLLECTION AND CHOICE EXPERIMENTS

Variety	Name	Origin, seeds color
1	Its 2 Sint. A1# Bulk	PR-99-A 761-A yellow
2	Its 2 Sint. A1# Bulk	PR-99-A 761-B white
3	Its 2 Sint. B3# Bulk	PR-99-A 761-B white
4	Its 2 Sint. A1# Bulk	PR-98-B 5766-A yellow
5	Its 2 Sint. B1# Bulk	PR-98-B 5766-B white
6	P36 C9 HC60-B-1-BBBBBBBBB-2 CL-03618	PR-99 A 402-16 yellow
7	CML287(P24F26*P27F1)-4-1-B-1-1-BB-F-####-BBB	PR-98 A 479-11 yellow
8	CL-00331SINT.AM.TSR-23-3-2-3-2-BB-F-##-B-B CML413	PR-98 A 474-16 yellow

The solitary endoparasitoid *C. marginiventris* that was used in the experiments originated from the USDA-ARS, Biological Control and Mass Rearing Research Unit. For the rearing of parasitoids, 25 young caterpillars (3–4 days old) were offered to a single mated female (4–7 days old) for 3 hr in a plastic box (9.5 cm diam., 5 cm high). The caterpillars were further reared on artificial diet in an incubator (25°C and 16L:8D) until cocoon formation. Cocoons were kept in Petri dishes until adult emergence. Emerging adults were sexed and kept in cages (30 × 30 × 30 cm) at a male–female ratio of 1:2, with distilled water on cotton and honey as a food source. The cages were kept in the laboratory under ambient light and temperature conditions.

Volatile Collection. After treatment and light exposure, plants were placed in a climate chamber (CMP4030, Conviron, Winnipeg, Canada) and the emitted volatiles were collected. The climate chamber was programmed at 20°C and with a light intensity of 14,500 lumens/m^2 (light provided by 28 lamps, 16 Sylvania 150-W VHO Cool White and 12 Sylvania 100-W Satin). Volatiles were collected from six plants simultaneously in an automated collection system as described by Heath and Manukian (1992) and Turlings et al. (1998). Glass cylinders (9.5 cm diam., 54 cm high) were placed over the plants and rested on a Teflon disk consisting of two halves with a hole in the middle for the stem of the plant. Air was pushed (1 liter/min) through a charcoal filter and introduced from the top of each cylinder over the plants. Super-Q traps (25 mg, 80/100 mesh, Alltech, Deerfield State) were attached laterally at the base of each cylinder. Traps were connected to an automated volatile collection system (ASU, ARS, Gainesville, Florida) through which the air was pulled out at 0.8 liters/min during 2 hr. The collection period was programmed with the use of the software TESS (Version 1.0, ARS, Gainesville, Florida). After each collection, volatiles were extracted from the traps with 150 μl methylene chloride, and 200 ng of *n*-octane and nonyl acetate were added as internal standards. Aliquots (3 μl) of the samples were injected on column, with an automated injection system into a Hewlett Packard model HP 6890 gas chromatograph equipped with a flame ionization detector. The apolar EC-1 capillary column (30 m × 0.25 mm ID, 0.25 μm film thickness, Alltech Associates) was held at 50°C for 3 min and then programmed at 8°C per min to 230°C, where it was maintained for 9.5 min. The column was preceded by a deactivated retention gap (10 m × 0.25 mm ID, Connex) and a deactivated precolumn (30 cm × 0.530 mm ID, Connex). Helium (24 cm/sec) was used as carrier gas. We collected and analyzed the odor of treated cowpea and maize plants ($N = 6$) as well as of 8 Mexican varieties ($N = 5$ for each variety). Hewlett Packard GC Chemstation software was used to quantify all major components by comparison to the known quantity of internal standards. Initial identification of most compounds was based on comparisons of retention times from previous studies (Turlings et al., 1998; Bernasconi et al., 1998). Conformation of identity by comparison of retention times with the synthetic samples was obtained for nerolidol (Fluka), (*E*)-β-farnesene (Denka

International), geranyl acetate (Fluka), (*Z*)-3-hexenol (Fluka), (*Z*)-3-hexenyl acetate (Sigma), linalool (Fluka), indole (Fluka), and β-myrcene (Sigma). A few compounds were identified only with the use of the Wiley library after mass spectrometry analysis (Agilent 5973, transfer line 230°C, source 230°C, quadrupole 150°C, ionization potential 70 eV, scan range 0–400 amu). These compounds are 2-hexenol, β-sesquiphellandrene, β-bisabolene, and cycloisosativene/α-ylangene. These identifications are regarded as tentative and are marked as such in the remainder of the text.

ANOVA and Student-Newman-Keuls *post-hoc* test were used to compare the total quantity of volatiles emitted among varieties (data ln-transformed). The Mann-Whitney test was used to compare differences in total emissions between plant species and among single compounds emitted by the different species and plant varieties. Tests were carried out with the program SPSS 10.0 for Windows.

Choice Experiments. A Y-shaped olfactometer was used to test the attractiveness of plant odors to *C. marginiventris* females. The system, based on a design by Sabelis and Van de Baan (1983), consisted of a central tube (13.5 cm long, 4 cm diam.) and two lateral arms (12 cm long, 4 cm diam.) ending with a glass frit (to create a homogeneous airflow and to prevent escape of test insects). The lateral arms tapered off into 0.5-cm tubes to which Teflon tubing was connected. Teflon tubes were used to introduce the odors into the Y-tube. To limit visual distractions for the insects, the Y-tube olfactometer was placed inside a white paper box, which was open on top (for illumination) and on the front side (for observation). An office lamp (60 W, 750 lumens/m^2) illuminated the olfactometer. A black and white striped pattern for visual orientation was placed under the Y-tube. Plants, treated and incubated in the same way as for volatile collections, were placed in plastic bags that were then heat-sealed. Humidified and purified (with activated charcoal) air was pushed into each bag via Teflon tubing and airtight connectors at pot height. The air passed over the plants and into the Teflon tubes connected with the arms of the olfactometer at a rate of 0.8 liters/min.

Wasps were used only one time and released singly at the base of the central arm of the Y-tube. In a first experiment, they were offered the odor of induced cowpea and maize (var. Delprim). In subsequent experiments, they had the choice between the odor of two different induced Mexican maize varieties. Twelve of the 36 possible combinations of the eight Mexican varieties were randomly chosen for these tests. It was not our goal to determine which of the eight varieties were the most attractive, but to establish if only the quantity or also the quality of the blends were important for the attraction of *C. marginiventris*. Naïve (no experience with hosts or plants) wasps were placed individually in the base of the olfactometer and observed for 10 min. If a wasp did not make a choice after this period, it was removed and recorded as a "no choice." Wasps that walked to the end of one of the arms and stayed there at least 5 secs were recorded as having made a choice for the odor offered through that arm. After four to seven individuals were tested,

the olfactometer was turned such that the direction of the arms was reversed and another four to seven wasps were tested. Each combination of odor sources was tested six to nine times with different plants and on different days. Each time the position of the two different odor sources was switched. A minimum of 67 and maximum of 94 wasps were tested in the 12 combinations of maize odor sources.

A binomial test was used to determine significant preferences for an odor. The number of wasps that chose the highest and lowest volatile emitting maize varieties on each experimental day was compared with a Wilcoxon signed rank test. This test was carried out using data of all experimental days to determine if the quantity (regardless of quality) of the odor was important for the attraction of the wasps.

RESULTS

Volatile Collection. The two plant species, cowpea and maize, differed dramatically in the quantities of volatiles emitted (Figure 1). The total amount of volatiles collected during the experiment was almost 53 times higher in maize (4141.35 ± 460.2 ng/2 hr) than in cowpea (77.9 ± 20.9 ng/2 hr) ($N = 6$, Mann-Whitney test: $P = 0.004$, $Z = -2.882$). The two plant species released several identical compounds, but cowpea did not release benzyl acetate, phenethyl acetate, 1-H-indole, (E)-β-caryophyllene, "β-sesquiphellandrene," or (E, E)-4,8,12-trimethyl-1,3,7,11-tridecatetraene, and it released only traces of (Z)-3-hexenyl acetate, (E)-β-ocimene, α-(E)-bergamotene, (E)-β-farnesene, "β-bisabolene," and nerolidol (Figure 1). In contrast, cowpea emitted considerable amounts of (E)-2-hexenal and significantly more (Z)-3-hexenol than maize plants (Figure 1).

Among the Mexican maize varieties we also found differences in the total amounts of volatiles collected ($N = 5$, ANOVA: $df = 7$, $F = 10.589$, $P < 0.001$, Figure 2). Variety 1 emitted 14 times more than variety 8 (Figure 2). We compared the emissions of volatiles for the varieties that were shown to be differentially attractive to *C. marginiventris* (see below). Variety 4 released significantly more (Z)-3-hexenal, (Z)-3-hexenol, and phenethyl acetate than variety 7 (Figure 3A). Variety 4 did not release geranyl acetate or (E)-β-ocimene, and variety 7 did not release "cycloisosativene/α-ylangene" or "β-sesquiphellandrene" (Figure 3A). Variety 1 released significantly more (Z)-3-hexenyl acetate, (E)-4,8-dimethyl-1,3,7-nonatriene, benzyl acetate, phenethyl acetate, geranyl acetate, and "cycloisosativene/α-ylangene" than variety 6 (Figure 3B). Variety 6 did not release (Z)-3-hexenyl acetate, (E)-β-ocimene, benzyl acetate, or phenethyl acetate (Figure 3B). Variety 1 released significantly more linalool, benzyl acetate, phenethyl acetate, 1-H-indole, geranyl acetate, α-(E)-bergamotene, (E)-β-farnesene, and "β-sesquiphellandrene" than variety 5 (Figure 3C). Variety 5 did not produce "cycloisosativene/α-ylangene" (Figure 3C).
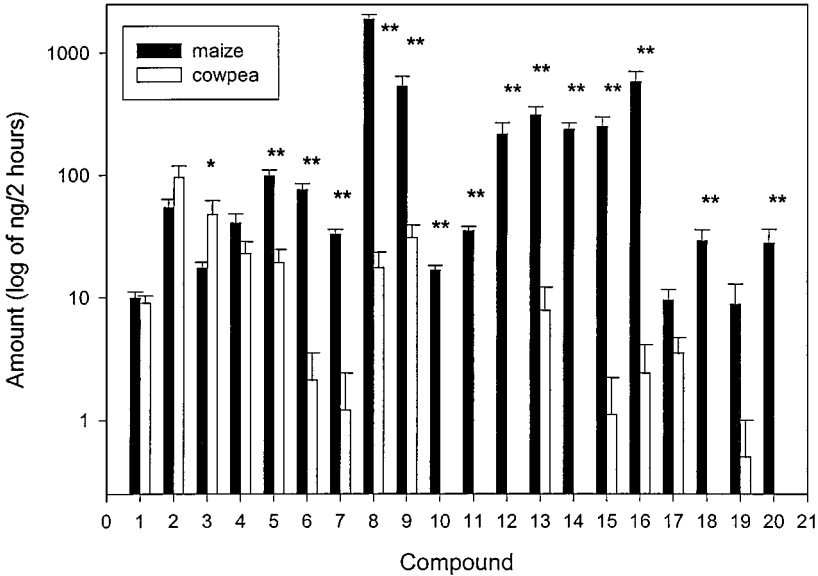
FIG. 1. Mean amount (±SE) of volatiles collected from cowpea and maize plants that were artificially damaged and treated with regurgitant of *Spodoptera littoralis* caterpillars. Collections started 5 hr after treatment and lasted 2 hr. Asterisks above bars indicate significant differences (Mann-Whitney test (two-tailed): $^*P < 0.05$, $^{**}P < 0.005$) in release of a specific compounds. The compounds are: **1**, 1-(*Z*)-3-hexenal; **2**, (*E*)-2-hexenal; **3**, (*Z*)-3-hexenol; **4**, "2–hexenol"; **5**, β-myrcene; **6**, (*Z*)-3-hexenyl acetate; **7**, (*E*)-β-ocimene; **8**, linalool; **9**, (*E*)-4,8-dimethyl-1,3,7-nonatriene; **10**, benzyl acetate; **11**, phenethyl acetate; **12**, 1-H-indole; **13**, geranyl acetate; **14**, (*E*)-β-caryophyllene; **15**, (*E*)-α-bergamotene; **16**, (*E*)-β-farnesene; **17**, "β-bisabolene"; **18**, "β-sesquiphellandrene"; **19**, nerolidol; **20**, (*E*,*E*)-4,8,12-trimethyl-1,3,7,11-tridecatetraene (compounds within quotation marks were tentatively identified by comparison of their MS-spectra with those of the Wiley library).

Choice Experiments. Cowpea odors were more attractive to *Cotesia marginiventris* than maize odors (Binomial test, $P = 0.007$, Figure 4). The parasitoids showed only a preference in 3 of the 12 combinations of Mexican maize varieties tested (Figure 4). In one case (var. 1 vs. var. 5), the wasps were attracted to the variety releasing more volatiles (Figures 2, 3C, and 4). However, in two cases (var. 4 vs. var. 7 and var. 1 vs. var. 6), the varieties tested released the same amounts of volatiles (Figures 2, 3A,B, and 4), and the preference must have been due to a difference in odor quality.

The number of wasps on each experimental day (89 experimental days in total) choosing the higher emitting maize variety on that day (mean ± SE wasps, 4.6 ± 0.25) was compared with the number of wasps on each experimental day choosing
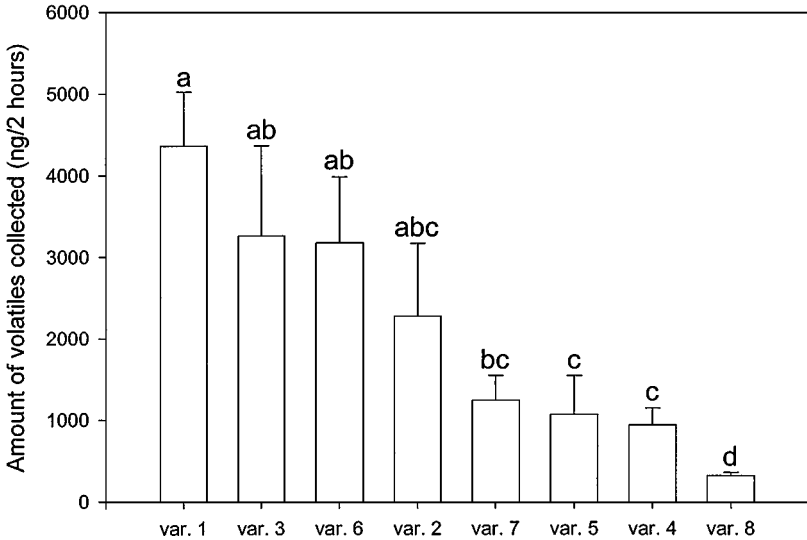
FIG. 2. Mean amount (±SE) of volatiles collected from different varieties of maize seedlings (10 days old) that were artificially damaged and treated with regurgitant of *Spodoptera littoralis* caterpillars. Volatiles were collected 6 hr after treatment, for 2 hr. Letters above bars indicate significant differences between varieties in the total amount released (Student-Newman-Keuls post hoc test after ANOVA: $df = 7$, $F = 10.589$, $P < 0.001$).

the lower emitting maize variety (3.8 ± 0.24 wasps). It revealed a marginally significant preference for the variety that emits larger amounts of volatiles offered in the dual choice test (Wilcoxon signed rank test: $P = 0.045$, $Z = -2.008$).

FIG. 3. Mean amount (±SE) of individual compounds collected from maize varieties that were artificially damaged and treated with regurgitant of *Spodoptera littoralis* caterpillars. Collections started 6 hr after treatment and lasted 2 hr. Asterisks above bars indicate significant differences (Mann-Whitney test (two-tailed): $^*P < 0.05$, $^{**}P < 0.005$, $^{***}P < 0.001$), between the two plant varieties (A: between varieties 4 and 7, B: 1 and 6, and C: 1 and 5). The compounds are: **1**, 1-(*Z*)-3-hexenal; **2**, (*E*)-2-hexenal; **3**, (*Z*)-3-hexenol; **4**, β-myrcene; **5**, (*Z*)-3-hexenyl acetate; **6**, (*E*)-β-ocimene; **7**, linalool; **8**, (*E*)-4,8-dimethyl-1,3,7-nonatriene; **9**, benzyl acetate; **10**, phenethyl acetate; **11**, 1-H-indole; **12**, geranyl acetate; **13**, "cycloisosativene/α-ylangene"; **14**, (*E*)-β-caryophyllene; **15**, (*E*)-α-bergamotene; **16**, (*E*)-β-farnesene; **17**, "β-sesquiphellandrene"; **18**, (*E*,*E*)-4,8,12-trimethyl-1,3,7,11-tridecatetraene (compounds within quotation marks were tentatively identified by comparison of their MS-spectra with those of the Wiley library).
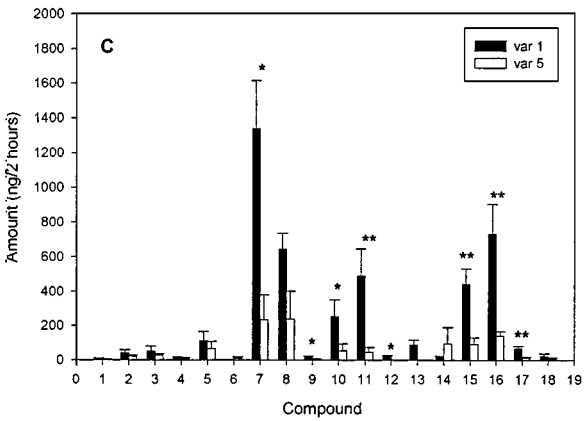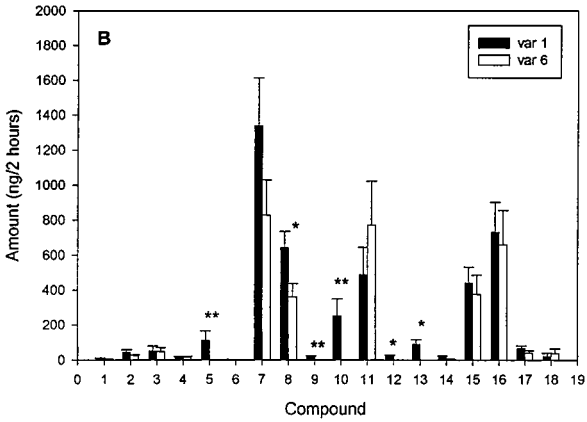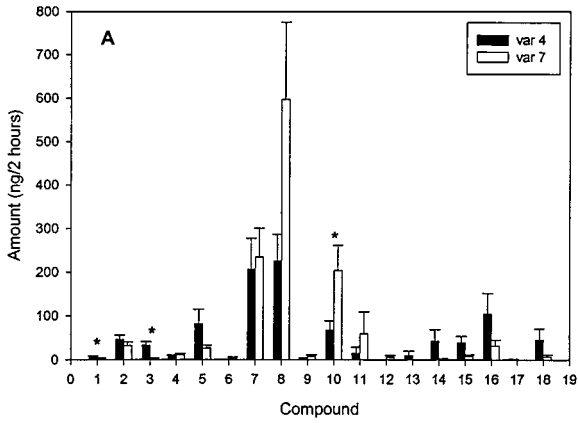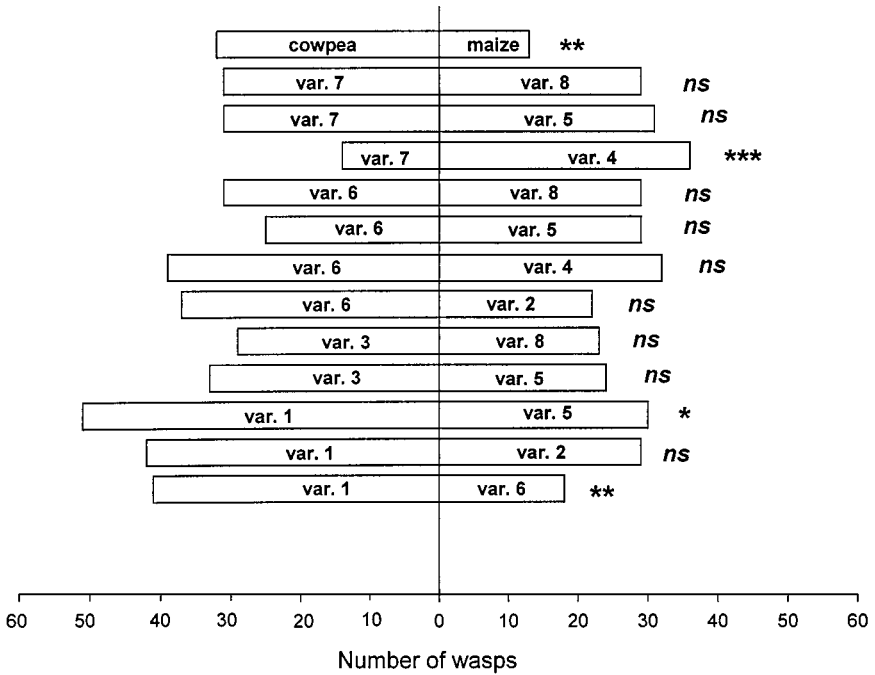
FIG. 4. Number of choices made by naïve *Cotesia marginiventris* in dual choice tests with various plant combinations offered in a Y-tube olfactometer. Asterisks indicate a significant difference within a choice test (*$P < 0.01$, **$P < 0.001$, ***$P < 0.0001$ and **ns** indicates no significant difference (binomial test).

DISCUSSION

Difference in Induced Volatile Emission among Plant Species and Varieties. Differences in herbivore-induced odor emissions among plant species genotypes have been demonstrated in several studies (Takabayashi et al., 1991, 1994a; Loughrin et al., 1995; Geervliet et al., 1997; Halitschke et al., 2000; Ozawa et al., 2000). In maize, these differences can be considerable (Gouinguené, et al., 2001). The current study confirms that different plant species, but also different varieties, release qualitatively and quantitatively different blends of induced odors. The 11 most important compounds that were collected from induced maize plants are partially shared with other plant species for which induced volatiles have been studied (Table 2). The only compound released by all plant species is (Z)-3-hexenol, and in 12 of 14 cases, (Z)-3-hexenyl acetate and (E)-4,8-dimethyl-1,3,7-nonatriene are also shared (Table 2).

TABLE 2. VOLATILES COLLECTED FROM REGURGITANT-INDUCED MAIZE PLANTS, SHARED AMONG OTHER PLANT SPECIES[a]

Compound	Apple	Bean	Brussels sprouts	Cabbage	Cucumber	Cotton	Gerbera	Pear	Potato	Soybean	Tobacco	Cowpea
1-(Z)-3-hexenal						+				+		+
(E)-2-hexenal	+(E?)	+	+	+		+		+		+		+
(Z)-3-hexenol	+	+	+	+	+	+	+	+	+	+		+
2-hexenol	+	+	+			+		+	+		+	+
β-myrcene	+(β?)		+	+(β?)		+(β?)	+(β?)					+
(Z)-3-hexenyl acetate	+	+	+	+	+	+	+	+		+		+
(E)-β-ocimene	+	+			+	+	+(Z)	+				+
linalool	+	+		+				+	+		+	+
(E)-4,8-dimethyl-1,3,7-nonatriene	+	+	+	+	+	+	+(Z)	+	+		+	+
benzyl acetate												
phenethyl acetate												
1-H-indole				+		+	+			+		
geranyl acetate							+					+
(E)-β-caryophyllene	+(E?)					+	+	+(E?)	+		+	
(E)-α-bergamotene							+		+		+(Z)	+
(E)-β-farnesene	+(E?)		+(α-)		+((E,E)-α)	+(γ-)	+	+(α)	+		+((E,E)-α)	+
β-bisabolene							+		+			
β-sesquiphellandrene							+		+			
nerolidol												+
(E,E)-4,8,12-trimethyl-1,3,7,11-tridecatetraene	+	+	+	+	+	+	+(di-)		+			

We found large qualitative and quantitative differences in induced odor blends between the plant species, maize and cowpea, and to a lesser extent among different maize varieties. Cowpea released almost exclusively green leaf volatiles, as was found by Whitman and Eller (1990), and maize released more indole, linalool, and a range of terpenoids that differed in the presence, proportion, and amount among varieties. Among maize varieties, the difference in total emission of volatiles was striking, with a 14-fold difference between lowest and highest emitting variety. When comparing the odors released by plants infested by *Pieris* larvae, Geervliet et al. (1997) showed differences in odor blends released by different plant species and cabbage varieties. Takabayashi et al. (1991, 1994a) found a qualitative and quantitative difference in volatile compounds emitted between two varieties of apple attacked by the same spider mite. In a comparison of *Spodoptera exigua*-infested leaves from different cotton varieties, naturalized cotton released seven times more volatiles than commercial cultivars (Loughrin et al., 1995). One constraint of using insects to induce odor emissions is that observed differences could be due simply to the fact that herbivores eat more or less of a specific plant species or variety. Using elicitors may allow for a more precise comparison. This was done by Halitschke et al. (2000), who treated the leaves of three genotypes of *Nicotiana attenuata* with methyl jasmonate and found a difference in the pattern of emitted compounds. The standardized treatment of the Mexican maize varieties in our study rules out any variable treatment effects. The results corroborate the tremendous variability in induced odor emissions in the genus *Zea* (see Turlings et al., 1998; Gouinguené et al., 2001).

Responses of Natural Enemies to Plant Odors. It is known that parasitoids show innate preferences to odors of specific undamaged plant species (Ngi-Song et al., 1996; Vaughn et al., 1996; Benrey et al., 1997). Furthermore, parasitoids show innate preferences for odors of specific plant varieties. For example, the parasitoid *Campoletis sonorensis* was attracted differentially to odors released by different cotton varieties (Elzen et al., 1986). In contrast, the parasitoid *Diaeretiella rapae*, did not distinguish among six grass varieties presented in a flight tunnel assay (Vaughn et al., 1996). If plants are damaged by herbivores, odors subsequently produced and released by the plants are considerably more attractive to parasitoids than odors of undamaged plants (Turlings et al., 1991b; Steinberg et al., 1993; Blaakmeer et al., 1994; Agelopoulos et al., 1995; Finidori-Logli et al., 1996; Bertschy et al., 1997; Cortesero et al., 1997; Röse et al., 1998). Choice experiments carried out in flight tunnels and in semi-field plots show that parasitoids have preferences for specific herbivore-attacked plant species (Drost et al., 1988; Geervliet et al., 1996; Du et al., 1998; De Moraes and Lewis, 1999).

Our study compared the attraction of *C. marginiventris* females to cowpea and maize and among maize varieties, focusing exclusively on odor cues. Cowpea odors were preferred over maize odors by naïve *C. marginiventris* females. This was somewhat surprising because cowpea released much less than maize. We had

expected the quantity of odors to be positively correlated with attractiveness, as is indicated by dose-dependent responses of natural enemies in several studies (Eller et al., 1988; Turlings et al., 1990a, 1991b; Ngi-Song et al., 1996; Vaughn et al., 1996; Weissbecker et al., 1999). Although the dual-choice experiments with maize varieties showed that, in general, *C. marginiventris* is more attracted to high releasing maize varieties, in a few combinations females showed preferences even if the quantities of odors produced by the two varieties did not differ. These results indicate that some compounds are more important than others for attraction of wasps, and that the proportions among compounds in the blend could play an important role. Cowpea released relatively larger proportions of green leaf volatiles as (*Z*)-3-hexenol, a very common compound among plant-induced volatiles (Table 2), than maize. Cortesero et al. (1997) analyzed the responses of *C. marginiventris* females to cotton plants and suggested that they primarily cue in on recently damaged plants, which are known to release green leaf volatiles. Other parasitoids like *Microplitis croceipes* and *Netelia heroica* are also attracted to green leaf volatiles, especially to different hexenols and hexenals, when they are offered individually in a flight tunnel (Whitman and Eller, 1990). The parasitoid *Aphidius rhopalosiphi* was strongly attracted to the two green leaf volatiles (*Z*)-3-hexenyl acetate and (*E*)-2-hexenal in Y-tube experiments (Wickremasinghe and Van Emden, 1992). These same chemicals are involved in the attraction of *C. glomerata* to infested or regurgitant-treated cabbage plants (Mattiacci et al., 1994). Green leaf volatiles are probably the most common volatiles released by plants damaged by herbivores (Table 2), which could explain why natural enemies without previous experience (naïve) are strongly attracted to them. (*Z*)-3-hexenol, which is shared by all plant species listed in Table 2, elicits strong responses in the two-spotted stinkbug predator *Perillus bioculatus*, while β-caryophyllene, a terpenoid shared by half of the plant species, elicited only weak responses (Weissbecker et al., 1999). Yet, the importance of specific plant volatiles and mixtures of volatiles has been suggested for the attraction of some natural enemies. The lacewing *Chrysopa carnea*, a predator of small insects, was caught more often in traps containing β-caryophyllene, than in traps that contained limonene, bisabolene, or caryophyllene oxide (Flint et al., 1979). In contrast, β-caryophyllene did not elicit antenna palpation by the parasitoid *Campoletis sonorensis*, whereas caryophyllene oxide did (Elzen et al., 1984). The EAG response of the two spotted stinkbug *Perillus bioculatus* was strong for a α-zingiberene and bicyclogermacrene mixture, but low/when these two compounds were offered singly to the predator (Weissbecker et al., 2000). The volatile compound borneol, extracted from garry oak, *Quercus garryana*, attracted the tachinid parasitoid *Cyzenis albicans* (Roland et al., 1995).

Innate Versus Learned Responses. Generally, naïve females respond poorly to odor cues, but a contact experience with hosts and/or host feces increases this responsiveness (Dmoch et al., 1985; Wardle and Borden, 1989; Whitman and Eller, 1990; Steinberg et al., 1992). These experiences can increase the insects'

motivation to search for a host, but this is also the result of associative learning of the encountered odors (Turlings et al., 1990b, 1993b; Vet and Groenewold, 1990). *C. marginiventris* females also show a dramatic increase in responses to herbivore-damaged maize plants in a flight tunnel after the females have contacted a host-damaged plant (Turlings et al., 1989, 1990b, 1993b). The olfactometer assays allowed us to better test odor preferences in naïve females. The strong responses to cowpea indicate that the innate preference is for the most common herbivore-attacked plant volatiles, the green leaf volatiles. Once a host is encountered, typical host-induced volatiles, like specific terpenoids, may be associated with host-presence, and the wasps will use these more reliable cues in searching for more hosts (Vet and Dicke, 1992). The fact that naïve females are less responsive to specific odor cues could explain why we found only three clear preferences among the 12 combinations tested in the Y-tube olfactometer. Nevertheless, the results suggest that *C. marginiventris* has some innate preference for certain odor blends. To reveal the key compounds in these blends, it would be useful to test the response of the parasitoids to plants that differ only in a single compound as suggested by Dicke and van Loon (2000).

Selection of Varieties and Wasps for Their Use in Biological Control. The selection of varieties that are highly attractive to parasitoids or selection of parasitoids that are particularly responsive to specific odors could be used to enhance biological control programs, as suggested by Loughrin et al. (1995) and Bottrell and Barbosa (1998). The exploitation of parasitoid associative learning in pest management has also been suggested (Wardle and Borden, 1985; Lewis and Martin, 1990; Papaj and Vet, 1990; Vet and Groenewold, 1990).

Some of the Mexican maize varieties tested here appear to be more attractive than others. Field studies will demonstrate if these differences in attractiveness are reflected in parasitism rates. The high genetic variability observed in odor emissions among maize lines (Gouinguené et al., 2001) make it an ideal plant to optimize its attractiveness.

In summary, we confirmed that there are qualitative and quantitative differences in herbivore-induced odor blends among maize varieties. Both quality and quantity of the volatile blends were important for the attraction of inexperienced *C. marginiventris*. Based on the results, we speculate that green leaf volatiles, which are the most common volatiles produced by herbivore-damaged plants, could be important for the attraction of naïve generalist parasitoids such as *C. marginiventris*. More specific compounds, such as terpenoids, could be learned associatively during host encounters. However, further studies will have to establish precisely which compounds are responsible for the observed differences in attractiveness and if such differences can be used to enhance biological control.

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