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Comparing the attraction of two parasitoids to herbivore-induced volatiles of maize and its wild ancestors, the teosintes

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Abstract Artificial selection of crop plants for desired traits such as increased yield and improved seed or fruit quality has been hypothesized to have had a cost for other potentially useful traits, including resistance to herbivores. Besides direct defences, such as the production of toxins, plants may also indirectly protect themselves by emitting volatile organic compounds (VOCs) that attract the natural enemies of herbivores. Parasitoid wasps are known to use these VOCs to localize hosts for their offspring. However, domestication and selective breeding of crop plants have reportedly led to the loss of such signals. The aim of this study was to identify possible differences in the attraction of parasitoid wasps by modern maize and its wild ancestors, the teosintes. In a six-arm olfactometer, we compared the capacity of teosintes and maize to attract the parasitoid wasps *Cotesia marginiventris* (Hymenoptera: Braconidae) and *Campoletis sonorensis* (Hymenoptera: Ichneumonidae). We studied the attractiveness of plants in which VOC emission was induced by the application of artificial damage and caterpillar regurgitant, as well as the attractiveness of extracts of volatiles that we collected from plants exposed to herbivory. *C. sonorensis* did not distinguish between the odours of maize and teosintes, whereas *C. marginiventris* showed a significant preference for the odours of teosintes over the odours of maize. The fact that we obtained very similar results with extracts of collected volatiles implies that we could use these extracts to identify the key compounds that are responsible for wasp attraction. Restoring and/or enhancing such key parasitoid attractants in cultivated plants could be an effective way to increase natural pest control.

Keywords *Campoletis sonorensis* · *Cotesia marginiventris* · Indirect plant defences · *Spodoptera frugiperda* · *Spodoptera littoralis* · Teosinte · Tritrophic interactions · Volatile organic compounds · *Zea mays*

Introduction

Artificial selection of crop plants for desired traits such as increased yield and improved seed or fruit quality can negatively influence other agronomically important traits, such as resistance to herbivores (Wink 1988; Welter and Steggall 1993; Rosenthal and Dirzo 1997; Rodriguez-Saona et al. 2011). On the one hand, selective breeding has caused a genetic bottleneck, reducing genetic diversity throughout the genome of domesticated crops, which is

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likely to result in weakening and losses of certain traits (Doebley et al. 2006). Moreover, resistance traits against insect feeding may be costly. Therefore, they may have been unconsciously selected against during domestication and/or artificial selection in favour of other, more tangible traits (Walters and Heil 2007; Chen et al. 2015). On the other hand, toxins that protect against insect feeding may have actively been selected against to increase palatability (Heaney et al. 1987; Paris 1989; Johns and Alonso 1990; Nee 1990; Enneking and Wink 2000).

Chemical defences represent an important mechanism with which plants can protect themselves against insect herbivores. The production of compounds with toxic or antifeedant effects is considered a direct defence response, as it has a direct negative effect on insect feeding (Howe and Jander 2008). In addition, plants may indirectly defend themselves with the emission of volatile organic compounds (VOCs) that can be used as foraging cues by natural enemies of herbivores in their search for prey or hosts (Dicke and Sabelis 1988; Turlings et al. 1990; Turlings and Wäckers 2004). Several domesticated plants appear to be less resistant to herbivory than their wild ancestors, including maize, cranberry and lupin (Wink 1988; Rosenthal and Dirzo 1997; Rodriguez-Saona et al. 2011). A small but increasing number of studies suggest that plant domestication has also influenced complex tritrophic interactions in various ways (Benrey et al. 1998; Chen and Welter 2002, 2003, 2005; Wang et al. 2009; Gols et al. 2011; Chen et al., 2015). This has not yet been studied in detail for maize.

The wild ancestor of modern maize, *Zea mays* L. ssp. *mays*, is Balsas teosinte, *Z. mays* ssp. *parviglumis* Iltis and Doebley (Matsuoka et al. 2002). Maize was first domesticated *c.* 9000 years ago as a single event in southern Mexico, where teosintes can still be found (Matsuoka et al. 2002). The plants grow in isolated populations, and also as weeds in maize fields (Sánchez González and Ruiz Corral 1995). The term teosinte is used for all taxa that comprise the genus *Zea* besides maize. The genus *Zea* contains a total of eight taxa classified into two sections and five species (Doebley and Iltis 1980; Iltis and Doebley 1980; Doebley 1990; Iltis 2000; Iltis and Benz 2000), although new classifications are continuously being proposed (Fukunaga et al. 2005; Sánchez González et al. 2011). We chose to study two teosintes that are closely related to modern maize: Balsas teosinte (*Z. mays* ssp. *parviglumis*) and Central Plateau teosinte (*Z. mays* ssp. *mexicana* (Schrader) Iltis). A previous study reported significant differences in total induced volatile emissions between *Z. mays* ssp. *mexicana* on the one hand and *Z. mays* ssp. *parviglumis* and maize variety Delprim on the other hand (Gouinguené et al. 2001).

It has been suggested that maize is less defended against insect feeding than teosintes as a result of domestication and artificial selection (Rosenthal and Dirzo 1997; Takahashi et al. 2012; Dávila-Flores et al. 2013). Recently, it was found that selective breeding has also disrupted VOC-mediated tritrophic interactions in maize. When attacked by the root-feeding larvae of the beetle *Diabrotica virgifera virgifera* LeConte (Coleoptera: Chrysomelidae), maize roots emit the volatile (*E*)-β-caryophyllene that attracts entomopathogenic nematodes (Rasmann et al. 2005). Interestingly, most American maize varieties have lost the ability to release this key nematode attractant, making their roots much more vulnerable to *Diabrotica* damage. The loss of (*E*)-β-caryophyllene emission appears to be the result of the lack of the expression of an (*E*)-β-caryophyllene synthase gene (Rasmann et al. 2005; Köllner et al. 2008). By transforming a deficient maize line with an (*E*)-β-caryophyllene synthase gene that was obtained from oregano, the volatile signal could be restored, thereby enhancing the protection that nematodes provide to the roots (Degenhardt et al. 2009). Similarly, commercial maize varieties have lost the ability to emit parasitoid-attracting VOCs in response to egg deposition by the stemborer moth *Chilo partellus* Latreille (Lepidoptera: Crambidae). This ability is naturally present in teosintes (Mutyambai et al. 2015) and is retained in maize landraces, locally adapted varieties that have been selected by farmers (Tamiru et al. 2011). Restoring and/or optimizing the release of the attractants in cultivated plants could therefore be an effective way to control pests (Bottrell et al. 1998; Cortesero et al. 2000; Turlings and Ton 2006).

For the current study, we included herbivorous and parasitoid insects that have a long evolutionary history with teosinte and maize. *Spodoptera frugiperda* Smith (Lepidoptera: Noctuidae) or fall armyworm is an important pest of maize in the Southern USA, Mexico, Central and South America (Luginbill 1928; Ortega 1987; Steffey et al. 1999; Farias et al. 2008). It is a highly polyphagous species with a strong preference for grasses (Luginbill 1928). Besides on maize, it is also frequently observed on teosinte (Luginbill 1928; Mondragón-Pichardo and Vibrans 2005; De La Paz Gutiérrez et al. 2010; Jofre y Garfias et al. 2010; Takahashi et al. 2012; De Lange et al. 2014). The species is known to induce maize direct defences (Glauser et al. 2011) as well as VOC emission (Carroll et al. 2006; De Lange 2008). The solitary koinobiont endoparasitoids *Cotesia marginiventris* Cresson (Hymenoptera: Braconidae) and *Campoletis sonorensis* Cameron (Hymenoptera: Ichneumonidae) are important natural enemies of *S. frugiperda* in Mexico (Hoballah et al. 2004; Molina-Ochoa et al. 2004; Jourdie et al. 2008; Von Mérey et al. 2012). Both parasitoids are generalists that attack a wide variety of early instar lepidopteran larvae (Cave 1995; Bahena-Juárez 2008). Parasitized caterpillars consume considerably less leaf tissue than healthy larvae and die before pupating, potentially benefitting the plant (Fritzsche Hoballah and Turlings 2001). Females of both species are attracted to herbivore-induced maize VOCs in a six-arm olfactometer (Turlings et al. 2004; Tamò et al. 2006a; De Lange 2008).

Although it is known that there is considerable variability in the capacity of maize and teosinte plants to emit VOCs in response to herbivory (Gouinguené et al. 2001), no study has yet looked at how these wild and cultivated plants may differ in their attractiveness to parasitoids. Because modern maize seems to have lost the ability to respond to egg deposition (Tamiru et al. 2011) and many maize varieties have lost a belowground signal, known to be present in *Z. mays* ssp. *parviglumis* (Rasmann et al. 2005; Köllner et al. 2008), we hypothesized that aboveground caterpillar-induced attractants may also be reduced in modern maize and that parasitoid wasps would be more attracted to herbivore-induced VOCs of teosintes than to those of maize.

As a first test of this hypothesis, we compared modern maize variety Delprim, Balsas teosinte and Central Plateau teosinte for their capacity to attract parasitoid wasps. As a rearing of *S. frugiperda* was not yet established, we performed this experiment with the closely related species *Spodoptera littoralis* Boisduval (Lepidoptera: Noctuidae). Plant volatiles were collected to compare the blends released by maize and teosinte plants in response to induction with caterpillar regurgitant. Simultaneously, we studied the attractiveness of the volatile blends to *C. marginiventris* and *C. sonorensis* in a six-arm olfactometer. To compensate for the difference in biomass between maize and teosinte plants, and the resulting potential differences in VOC emission quantity, we conducted additional olfactometer studies using volatile extracts as olfactory stimuli. The volatile extracts were obtained by collecting the headspace of herbivore-attacked maize and Balsas teosinte plants, and the extracts were diluted to obtain a similar total VOC concentration. For these experiments, both *S. frugiperda* and *S. littoralis* were used as herbivores. We discuss our results in the context of crop protection.

Materials and methods

Plants

Maize (*Z. mays* ssp. *mays*, variety Delprim, European commercial hybrid; Delley semences et plantes SA, Switzerland), Balsas teosinte (*Z. mays* ssp. *parviglumis*, PI566691, Michoacán, Mexico; USDA-ARS, USA) and Central Plateau teosinte (*Z. mays* ssp. *mexicana*, PI566677, Michoacán, Mexico; USDA-ARS, USA) seeds were sown in plastic pots (4 cm diameter, 10 cm high) with fertilized commercial soil (Ricoter Aussaaterde, Aarberg, Switzerland). A representative picture of maize and teosinte seeds is shown in Online Resource 1. All plants were kept in a climate chamber (maize: 25 ± 2 °C; teosinte: 30 ± 2 °C; 60 % relative humidity; 16 h light/8 h dark; 50,000 lm/m^2). The teosintes—found within the tropical and subtropical areas of Mexico—required a slightly higher temperature than maize variety Delprim to germinate and grow well (ESdL, personal observations). At the start of the different experiments, the plants were 10- to 20-day old and had 2–3 fully expanded true leaves. For more information about genotypic and phenotypic differences between cultivated maize and teosintes, see Doebley et al. (1997) and Doebley (2004).

Insects

The caterpillars *S. littoralis* and *S. frugiperda* and the parasitoids *C. marginiventris* and *C. sonorensis* were reared as described by Turlings et al. (2004), Tamò et al. (2006a, b) and Maag et al. (2014). *S. frugiperda* larvae were obtained from an in-house colony and were reared on a chickpea flour-based artificial diet. *S. littoralis* larvae were reared from eggs provided by Syngenta (Stein, Switzerland). The eggs were kept in an incubator (25 °C, 16 h light/8 h dark) and after emergence larvae were placed on a wheat germ-based artificial diet at room temperature. To rear the parasitoid wasps, 25 *S. littoralis* caterpillars (3- to 4-day old) were offered to a single mated female (4- to 7-day old) for 3 h in a plastic box (9.5 cm in diameter, 5 cm height). The parasitized caterpillars were kept on a wheat germ-based artificial diet in an incubator (25 °C, 16 h light/8 h dark) until cocoon formation. Cocoons were kept in Petri dishes until adult emergence. The adults were sexed and kept in cages (30 × 30 × 30 cm) in an incubator (25 °C, 16 h light/8 h dark) at a sex ratio of 1:2 (male:female) with moist cotton wool and honey as a food source. *S. littoralis* regurgitant was collected from third- and fourth-instar larvae that had been fed on maize leaves, as described by Turlings et al. (1993).

Before a rearing colony of *S. frugiperda* became available, we performed experiments with the herbivore *S. littoralis*. This insect has been reported to feed on maize in Northern Africa and the Near East (Hill 1987). Although differences exist in the foraging patterns of *S. frugiperda* and *S. littoralis* on maize plants (Köhler et al. 2015), as well as the ways the insects cope with maize chemical defences (Glauser et al. 2011) and the quantities of maize volatiles that they may induce (De Lange 2008), both species induce a volatile blend of similar composition (De Lange 2008). Also, application of regurgitant of both species to wounded plants, as a means of artificial induction of defences, results in the emission of similar blends of VOCs (De Lange 2008). The two parasitoid species that were tested readily accept *S. littoralis* as a host and both are strongly attracted to *S. littoralis*-induced plant volatiles (Turlings et al. 2004; Tamò et al. 2006a, b).

Induction of plants

Odour emission in plants used for six-arm olfactometer bioassays was elicited by scratching the undersides of two leaves with a razor blade over an area of approximately 1 cm^2 on both sides of the central vein. Immediately after wounding, 10 µl of *S. littoralis* regurgitant was applied to the wounds. This treatment was performed 15 h as well as 1 h before the start of the experiments. Artificial damage instead of caterpillar-inflicted damage was applied to prevent bias in VOC emission due to differential feeding by the herbivores on maize and teosinte plants (Sandrine P. Gouinguené, unpublished data). For the collection of plant volatile extracts, plants were infested with 20-s instar *S. littoralis* larvae or 5-s instar *S. frugiperda* larvae the night prior to odour collections.

Plant volatile collection and analysis

Volatile collections from all three plant genotypes (maize variety Delprim, Balsas teosinte and Central Plateau teosinte) were conducted simultaneously, during the six-arm olfactometer bioassays with plants described below. Plants were placed in glass vessels into which purified air entered through a Teflon tube at a rate of 1.2 l/min. Air was pulled out of the vessels at a rate of 0.6 l/min through a trapping filter containing 25 mg of 80–100 mesh SuperQ adsorbent (Alltech Associates, Inc., Deerfield, Illinois, USA). Before each collection, these filters were rinsed with 3 ml dichloromethane (Suprasolv, GC-grade, Merck, Dietikon, Switzerland). Odour collections lasted for 3 h, and for each plant either one collection was performed in the morning (1–4 h after the last induction) or two collections were performed, one in the morning and one in the afternoon (4–6 h after the last induction, $n = 16$ odour collections on 11 individual plants). After each collection, the filters were removed and eluted with 150 µl of dichloromethane. Two internal standards (*n*-octane and nonyl acetate, each 200 ng in 10 µl dichloromethane) were added to each sample. The samples were stored at −80 °C before analysis (Turlings et al. 2004).

VOCs were analysed using an Agilent 6850 gas chromatograph with a flame ionization detector (GC-FID). A 3-µl aliquot of each sample was injected in pulsed splitless mode onto an apolar capillary column (HP-1 ms, 30 m, 0.25 mm ID, 0.25 µm film thickness; Agilent J&W Scientific, USA). Helium at constant pressure (18.71 psi) was used as carrier gas. After injection, the column temperature was maintained at 40 °C for 3 min, and then increased to 100 °C at 8 °C/min and subsequently to 200 °C at 5 °C/min followed by a post-run of 3 min at 250 °C. The detected VOCs were quantified based on a comparison of their peak areas with those of the internal standards and identified by comparison of retention times with those from previous analyses (D'Alessandro and Turlings 2005). After each VOC collection, plant shoots were harvested and fresh weight was determined.

To confirm the identities of the different peaks, at least one odour sample per plant genotype was analysed using a gas chromatograph (Agilent 6890 Series GC System G1530A) coupled to a mass spectrometer (GC–MS; Agilent 5973 Network Mass Selective Detector; transfer line 230 °C, source 230 °C, ionization potential 70 eV). An aliquot of 2 µl was injected in the pulsed splitless mode onto the same type of column as described above. Helium at constant flow (0.9 ml/min) was used as carrier gas. After injection, the column temperature was maintained at 40 °C for 3 min, and then increased to 100 °C at 8 °C/min and subsequently to 220 °C at 5 °C/min followed by a post-run of 3 min at 250 °C. The detected VOCs were identified by comparison of their mass spectra with those of the NIST05 library, by comparison of their spectra and retention times with those of authentic standards and by comparisons of retention times with those from previous analyses (D'Alessandro and Turlings 2005). Volatiles that met only one of these criteria were labelled as tentatively identified. Eleven dominating compounds were identified in the headspace of plants induced with *S. littoralis* regurgitant.

Preparation of volatiles in solution

Because Balsas teosinte is most closely related to modern maize (Matsuoka et al. 2002) and we confirmed the previous finding of Gouinguené et al. (2001) that cultivated maize and Balsas teosinte do not significantly differ in the total quantities of volatiles that they emit, only Balsas teosinte and maize variety Delprim were used in subsequent experiments. Plants were placed in a multiple air-delivery VOC collection setup as described by Turlings et al. (2004) and Ton et al. (2007). VOCs were collected in a similar way as in the six-arm olfactometer described below, using 200 or 150 µl of dichloromethane to elute the filters for *S. littoralis*-induced volatile extracts and *S. frugiperda*-induced volatile extracts, respectively. No internal standard was added. Three collections of 3 h were performed on each day. The eluted samples of all individual collections, here referred to as volatile extracts, were combined for maize and for teosinte separately and were stored at −80 °C before analysis. Two 150-µl samples of the maize and teosinte volatile extracts were analysed by means of GC-FID as described above. The relative peak area of the 30 dominating compounds was calculated. We corrected for VOC abundance by diluting the most concentrated extract with dichloromethane, so that the two extracts had a similar total VOC concentration. Twenty-six out of the 30 dominating compounds could be (tentatively) identified in the volatile extracts of *S. frugiperda*-damaged plants.

Six-arm olfactometer bioassays with plants

Bioassays were performed in a six-arm olfactometer as described by Turlings et al. (2004). Maize, Balsas teosinte and Central Plateau teosinte plants were placed on randomized positions in the olfactometer on each experimental day. Three arms were left empty and arms with a plant were always alongside an arm without a plant. Whilst half of the incoming air that passed over the plants was pulled through trapping filters for odour collection, the other half entered the chamber where the wasps were released in groups of six. Mated 2- to 6-day-old female *C. marginiventris* and *C. sonorensis* wasps were given 30 min to make a choice for an arm, thereby revealing their preferences for the odour sources. The females were naïve, which means that as adults they had never been in contact with a plant or a host before. Three to eight releases in groups of six wasps were performed on each experimental day, on a total of 5–8 experimental days. Experimental days where >50 % of the wasps made a choice for an arm were included in the analysis ($n = 210$ for *C. marginiventris* and $n = 180$ for *C. sonorensis*, data of 1 experimental day were excluded for *C. marginiventris*). Because the response of *C. marginiventris* is known to be affected by the odour of *C. sonorensis* (Tamò et al. 2006b), the two species were tested in separate olfactometers.

Six-arm olfactometer bioassays with volatile extracts

An aliquot of 50 µl of maize or Balsas teosinte volatile extract was applied on a filter paper (Whatman grade no. 1), which was then rolled up and introduced into a clean glass tube. Control tubes contained filter paper treated with 50 µl of solvent (dichloromethane) only. The tubes containing volatile extracts were placed on opposite sides of a six-arm olfactometer that was adapted for application of the extracts (Fig. 1; D'Alessandro and Turlings 2005; D'Alessandro et al. 2009). Experiments began about 15 min after assembling the olfactometers, testing mated, naïve 2- to 7-day-old female *C. marginiventris* and *C. sonorensis* wasps. Experimental days where >50 % of the wasps responded were included in the analysis (*S. littoralis*-induced volatile extracts: $n = 252$ for both wasp species, data of 2 experimental days were excluded for *C. marginiventris*; *S. frugiperda*-induced volatile extracts: $n = 108$ for *C. marginiventris* and $n = 96$ for *C. sonorensis*).

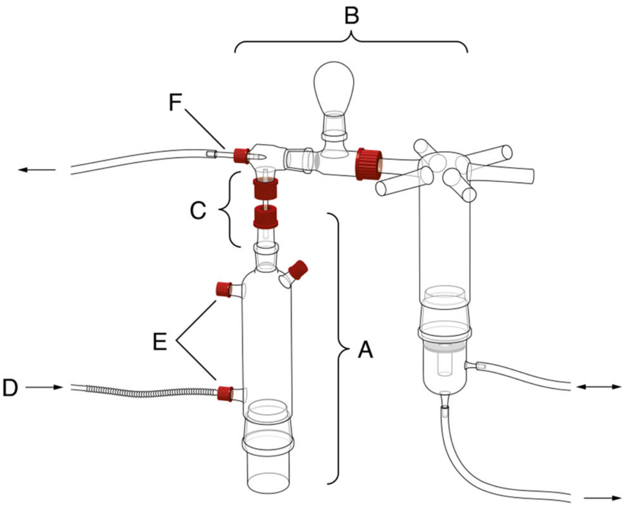

Fig. 1 An overview of the six-arm olfactometer, suitable to test the attractiveness of extracts of collected plant volatiles for parasitoid wasps. *A* glass bottle; *B* wasp central choice chamber and insect trapping bulb; *C* odour source, glass tube with filter paper containing maize or teosinte volatile extract; *D* air inlet; *E* teflon-coated GL-screwcap fittings; *F* volatile collection filter. Adapted from Turlings et al. (2004) and D'Alessandro and Turlings (2005)

Statistics

For all analyses of VOC emission data were $\log(x + 1)$-transformed. For analysis of VOC quantities (i.e. amounts), VOC emission data were tested for normality and homogeneity of variance prior to analysis using multivariate analysis of variance (MANOVA) with variety as factor. Multiple comparisons for individual compounds between varieties were tested using Tukey's post-hoc test (95 % confidence interval). Interspecific qualitative differences (i.e. the relative importance of the individual compounds in the composition of the odour blend) were tested using a similar approach on the relative amounts of individual compounds after empirical logistic-transformation (i.e. $\log(y + e/[1 - y + e]$, $e = 0.005$) according to Warton and Hui (2011). To assess the effect of time, VOC emission data were also analysed using MANOVA with time (morning or afternoon) as factor. To visualize differences between the volatile patterns of the different plants, the total volatile profiles were analysed using principal component analysis (PCA). For analysis of total VOC quantities (i.e. the total amount of all individual compounds), VOC emission data were analysed using one-way analysis of variance (ANOVA) and Holm–Sidak post-hoc test. Plant fresh weight data were analysed using one-way ANOVA and Holm–Sidak post-hoc test. The analyses were performed using Minitab version 17 (http://www.minitab.

com) and SigmaPlot version 12 (Systat Software, San Jose, CA, USA). Wasp choice data were analysed using a generalized linear model (GLM) fitted by maximum quasi-likelihood estimation according to Turlings et al. (2004). These analyses were performed in the software package R version 3.0.2 (R Core Team 2013).

Results

Volatile emission in maize and teosintes and plant fresh weight

The volatile profiles of maize, Balsas teosinte and Central Plateau teosinte differed significantly (MANOVA, $F_{(22,50)} = 10.98$, $P < 0.001$, Wilks' $\lambda = 0.023$, Table 1). Qualitative differences, i.e. relative proportions of the individual compounds in the odour blend, between the chemical profiles of maize and teosintes were also found (MANOVA, $F_{(22,36)} = 10.37$, $P < 0.001$, Wilks' $\lambda = 0.019$, Online Resource 2). All 11 identified compounds could be detected in headspace samples of the three plants, but the identities of the most abundant compounds differed: linalool was most abundant in the headspace of maize, (*E*)-β-farnesene was most abundant in the headspace of Balsas teosinte, and (3*E*)-4,8-dimethyl-1,3,7-nonatriene was most abundant in the headspace of Central Plateau teosinte. The PCA shows that the three plants emitted distinct patterns of volatiles. The first two principal components explained 71 % of the total variance (Fig. 2). Total volatile emissions varied markedly amongst the plants, with maize and Balsas teosinte emitting significantly larger amounts of volatiles than Central Plateau teosinte (one-way ANOVA, $F_{(2,43)} = 16.75$, $P < 0.001$; Fig. 3).

Slight differences between headspace samples collected in the morning, i.e. right after application of damage, and in the afternoon, i.e. a few hours after treatment, were observed (MANOVA, $F_{(11,26)} = 3.95$, $P = 0.002$, Wilks' $\lambda = 0.374$). In morning samples more (*Z*)-3-hexenyl acetate was detected, whilst afternoon samples contained more (*E*)-α-bergamotene. Most olfactometer tests were conducted in the morning, when all compounds were released in significant quantities.

Maize had a higher shoot biomass than its wild relatives (average shoot fresh biomass in mg ± SE: maize 187 ± 11.3a, Balsas teosinte 107 ± 9.5b, Central Plateau teosinte 123 ± 11.1b; one-way ANOVA, $F_{(2,30)} = 15.72$, $P < 0.001$; different letters indicate significant differences).

Six-arm olfactometer bioassays with plants

Both wasp species preferred the arms with the plants over the empty arms (GLM, $P < 0.001$; Fig. 4). Whilst *C. marginiventris* wasps were significantly more attracted to Balsas teosinte (GLM, $P < 0.01$) and to Central Plateau teosinte (GLM, $P = 0.01$) than to maize, they did not distinguish between the two teosintes (GLM, $P = 0.93$; Fig. 4a). *C. sonorensis* was not selectively attracted to any of the offered plants (GLM, $P > 0.05$; Fig. 4b).

Table 1 Absolute amount of volatile emission by one maize variety and two teosintes when induced with *Spodoptera littoralis* regurgitant (in ng/3 h/plant ± SE)

No.	Volatile organic compound	Class	Maize[a]	Balsas teosinte[b]	Central Plateau teosinte[c]
1	β-Myrcene	Monoterpenes	14.7 ± 1.8a	4.6 ± 0.5b	3.7 ± 0.5b
2	(*Z*)-3-hexenyl acetate	Esters (GLV)	114.3 ± 29.7a	37.0 ± 8.3ab	25.5 ± 6.5b
3	(*Z*)-β-ocimene	Monoterpenes	2.3 ± 0.5b	14.1 ± 5.0a	0.5 ± 0.2b
4	linalool	Monoterpenes	152.9 ± 24.1a	97.5 ± 17.1a	29.9 ± 11.5b
5	(3*E*)-4,8-dimethyl-1,3,7-nonatriene	Homoterpenes	44.8 ± 10.3b	136.1 ± 28.8a	63.1 ± 24.0b
6	Phenethyl acetate	Esters	5.3 ± 1.4ab	10.4 ± 2.7a	0.9 ± 0.4b
7	Indole	Aromatics	18.9 ± 4.3b	58.8 ± 11.8a	5.2 ± 2.6c
8	(*E*)-β-caryophyllene	Sesquiterpenes	6.1 ± 1.4a	38.2 ± 9.5a	4.4 ± 2.0b
9	(*E*)-α-bergamotene	Sesquiterpenes	41.1 ± 12.2ab	163.4 ± 40.4a	19.4 ± 9.3b
10	(*E*)-β-farnesene	Sesquiterpenes	61.2 ± 14.6ab	279.4 ± 51.1a	24.2 ± 9.4b
11	(3*E*, 7*E*)-4,8,12-trimethyl-1,3,7,11-tridecatetraene	Homoterpenes	3.1 ± 1.0b	18.4 ± 3.4a	4.7 ± 1.7ab

Different letters indicate significant differences (MANOVA followed by Tukey's post-hoc test 95 % confidence interval, $P < 0.05$)

GLV green leaf volatile

[a] *Zea mays* ssp. *mays*

[b] *Z. mays* ssp. *parviglumis*

[c] *Z. mays* ssp. *mexicana*

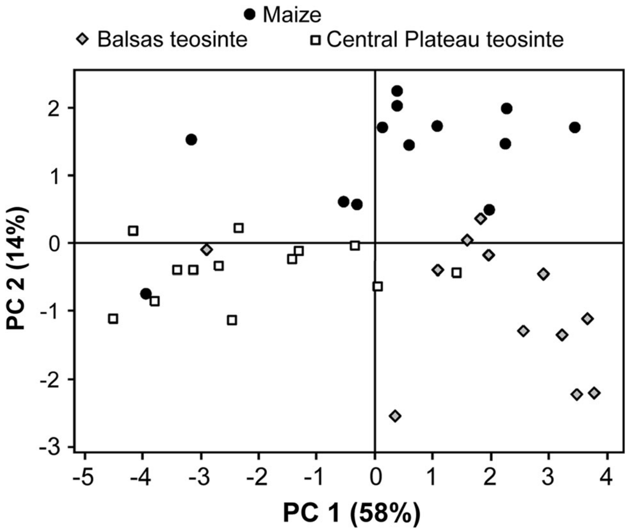

Fig. 2 Principal component analysis (PCA) of herbivore-induced plant volatile emissions. Three plant genotypes were compared, maize variety Delprim (*Zea mays* ssp. *mays*), Balsas teosinte (*Z. mays* ssp. *parviglumis*) and Central Plateau teosinte (*Z. mays* ssp. *mexicana*). Odour emission was induced by wounding and application of *Spodoptera littoralis* regurgitant. The PCA shows the first and second principal components (PC) with the explained variance in *brackets*

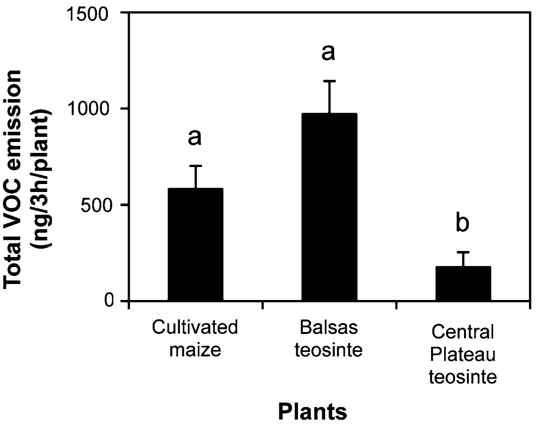

Fig. 3 Total volatile emissions by one maize variety and two teosintes when induced with *Spodoptera littoralis* regurgitant. Cumulative amount of the 11 dominating volatile organic compounds (+SE) as shown in Table 1. *Different letters* significant differences (one-way ANOVA followed by Holm–Sidak post-hoc test, $P < 0.001$)

Six-arm olfactometer bioassays with volatile extracts

Both wasp species preferred the arms that carried the odours of the extracts over the arms that contained solvent only (GLM, $P < 0.001$; Fig. 5). As with actual plants, *C. marginiventris* preferred the volatile extract of Balsas

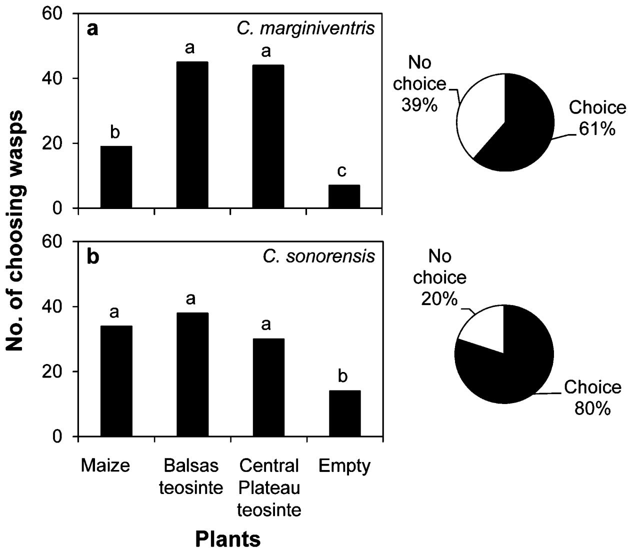

Fig. 4 Responsiveness of parasitoid wasps to herbivore-induced odour emissions of one maize variety and two teosintes. Odour emission was induced by wounding and application of *Spodoptera littoralis* regurgitant. **a** Choices made by *Cotesia marginiventris*. **b** Choices made by *Campoletis sonorensis*. Empty = control, empty vessels (average value of three vessels). *Pie charts* the proportion of wasps choosing an arm. *Different letters* significant differences (GLM, $P < 0.05$). Composition of the plant odours is displayed in Table 1

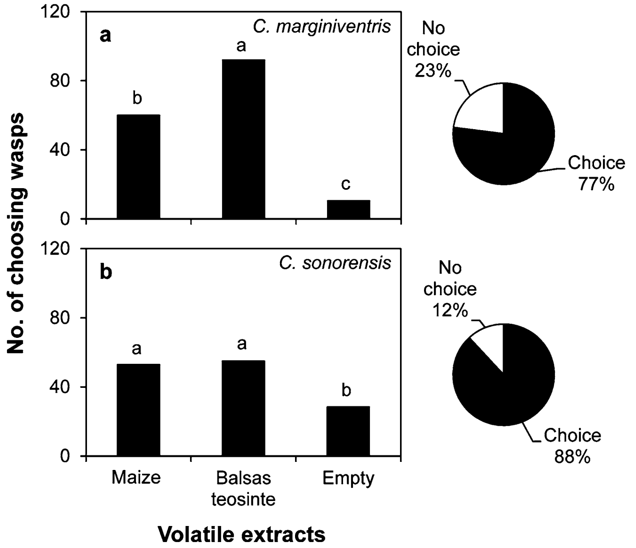

Fig. 5 Responsiveness of parasitoid wasps to extracts of volatiles of *Spodoptera littoralis*-induced maize and Balsas teosinte. **a** Choices made by *Cotesia marginiventris*. **b** Choices made by *Campoletis sonorensis*. Empty = control, empty vessels (average value of four vessels). *Pie charts* the proportion of wasps choosing an arm. *Different letters* significant differences (GLM, $P < 0.05$)

teosinte over the volatile extract of maize (GLM, $P = 0.01$; Fig. 5a), whereas *C. sonorensis* did not discriminate between the two odour blends (GLM, $P = 0.85$; Fig. 5b).

Six-arm olfactometer bioassays with *S. frugiperda*-induced volatile extracts

A representative chromatogram of volatile extracts of maize and teosinte is shown in Fig. 6. Both wasp species preferred the two arms that carried the odours of the volatile extracts over the four arms that contained solvent only (GLM, $P < 0.001$), even though the preference of *C. marginiventris* of maize extracts over control arms was not statistically significant (GLM, $P = 0.06$; Fig. 7). *C. marginiventris* females were significantly more attracted to herbivore-induced volatile extract of Balsas teosinte than of maize (GLM, $P = 0.008$; Fig. 7a). *C. sonorensis* females did not exhibit a preference for the odours of either maize or teosinte (GLM, $P = 0.74$; Fig. 7b).

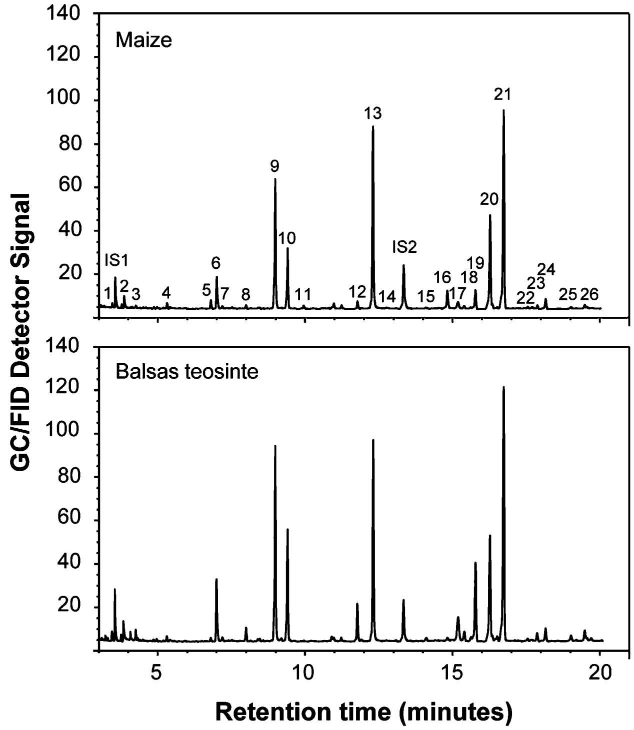

Fig. 6 Chromatograms of extracts of collected volatiles from *Spodoptera frugiperda*-damaged maize and teosinte plants. The labelled compounds are: 1 = (*Z*)-3-hexenal; 2 = (*E*)-2-hexenal; 3 = (*Z*)-3-hexenol; 4 = (*Z*)-2-penten-1-ol acetate^{N}; 5 = β-myrcene; 6 = (*Z*)-3-hexenyl acetate; 7 = (*E*)-2-hexenyl acetate; 8 = (*Z*)-β-ocimene; 9 = linalool; 10 = (3*E*)-4,8-dimethyl-1,3,7-nonatriene; 11 = benzyl acetate; 12 = phenethyl acetate; 13 = indole; 14 = unknown; 15 = methyl anthranilate; 16 = geranyl acetate; 17 = unknown; 18 = unknown; 19 = (*E*)-β-caryophyllene; 20 = (*E*)-α-bergamotene; 21 = (*E*)-β-farnesene; 22 = unknown sesquiterpenoid; 23 = unknown sesquiterpenoid; 24 = β-sesquiphellandrene^{N}; 25 = (*E*)-nerolidol; 26 = (3*E*,7*E*)-4,8,12-trimethyl-1,3,7,11-tridecatetraene. IS1 and IS2, internal standards (*n*-octane and nonyl-acetate). ^{N}Tentative identification. Extracts were not yet diluted to obtain a similar total VOC concentration; dilutions were based on the relative area of the 30 dominating compounds

Discussion

Our study shows that modern maize may have lost some of its signalling capacity important for indirect defence. The maize variety we tested, Delprim, emits upon herbivory an odour blend that is qualitatively and quantitatively different from that of its wild ancestor Balsas teosinte and closely related Central Plateau teosinte (Figs. 2, 3; Table 1, Online Resource 2). These results are in accordance with earlier findings showing variability in headspace composition of herbivore-induced maize and teosinte varieties (Gouinguené et al. 2001).

Eleven dominating compounds were consistently present in the blends emitted by caterpillar-damaged plants, as well as plants that were mechanically damaged and treated with regurgitant. Yet, caterpillar feeding was slightly more effective in inducing minor compounds, which in most cases were only detected in trace amounts after the artificial damage treatment. We chose to standardize damage by means of wounding and regurgitant application for initial experiments because it excludes potential confounding

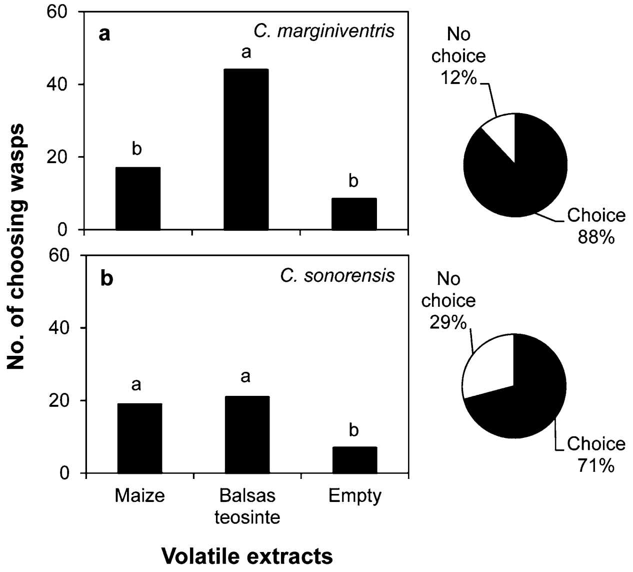

Fig. 7 Responsiveness of parasitoid wasps to extracts of volatiles of *Spodoptera frugiperda*-induced maize and Balsas teosinte. **a** Choices made by *Cotesia marginiventris*. **b** Choices made by *Campoletis sonorensis*. Empty = control, empty vessels (average value of four vessels). *Pie charts* the proportion of wasps choosing an arm. *Different letters* significant differences (GLM, $P < 0.05$). The preference of *C. marginiventris* of maize extracts over control arms was not statistically significant (GLM, $P = 0.06$). Composition of the plant volatile extracts is displayed in Fig. 6

effects linked to differences in herbivore feeding rate on the three plants. We also observed slight differences in the constituents of headspace samples collected from regurgitant-treated plants in the morning and in the afternoon; morning samples contained more green leaf volatiles (GLVs), whereas afternoon samples contained more sesquiterpenes. This confirms that, in maize, terpenoids are truly inducible and are emitted only several hours after initial damage, whereas GLVs are emitted upon fresh damage (Turlings et al. 1998). The olfactometer tests with plants were mostly conducted in the morning, when GLVs and sesquiterpenes—the combination of which is known to be highly attractive to *C. marginiventris* (Hoballah and Turlings 2005)—were released in significant quantities.

Interestingly, the two solitary endoparasitoids that were tested responded differently to the odours that they were offered, independent of whether the bioassays were performed with plants or volatile extracts and of whether the plants were induced by *S. frugiperda* or *S. littoralis*. Whereas *C. sonorensis* did not distinguish between different odour blends (Figs. 4b, 5b, 7b), *C. marginiventris* preferred the odours of the two teosintes to those of maize (Fig. 4a, 5a, 7a). These results confirm that, at least for *C. marginiventris*, the ecologically relevant differences between the odours of modern maize and teosintes are qualitative rather than quantitative (D'Alessandro et al. 2009). Previous studies that compared the behaviour of *C. marginiventris* and *C. sonorensis* revealed that naïve females of both wasp species are equally attracted to the odours of herbivore-induced maize, cotton and cowpea plants (Tamò et al. 2006b). However, electrophysiological (i.e. GC-EAG) recordings showed that the wasps are sensitive to many, but not all, compounds of the volatile blends and the intensity of responses to specific compounds varied greatly between species (Gouinguené et al. 2005). The wasps also displayed differences in their attraction to maize plants treated with two resistance elicitors (Sobhy et al. 2012). Altogether, these results imply that the two species orient towards different compounds in the volatile blend. Since both species co-occur throughout North America and compete for lepidopteran hosts (Tamò et al. 2006b), the differential use of available foraging cues may allow them to occupy different niches and reduce interspecific competition for hosts.

In line with our hypothesis, our results suggest that maize and teosinte emit odour blends that are differentially attractive, but only to one of the two parasitoids. It should be noted, however, that the observed differences in volatile emissions fall well within the range of the known variation amongst maize genotypes. Different maize and teosinte varieties vary markedly in their VOC-emission response towards herbivory (Gouinguené et al. 2001; Degen et al. 2004, 2012; Erb et al. 2011). Here, we show that this can impact the plants' attractiveness to parasitoids, although at this point we cannot generalize our results. Additional plant varieties and populations should be tested to determine if maize and teosinte plants consistently differ in their attractiveness to parasitoid wasps. Nevertheless, our results provide a first indication that during domestication and/or artificial selection, maize may have lost some of its ability to attract certain parasitoids.

Although it has proven to be very difficult to identify the bioactive compounds in a complex odour blend (D'Alessandro and Turlings 2006), in several model systems, "key compounds" have been identified that play an important role in natural enemy attraction (Du et al. 1998; Powell et al. 1998; De Boer and Dicke 2004; De Boer et al. 2004; Rasmann et al. 2005). In our experiments the wasps' responses remained unchanged when substituting actual plants with headspace extracts, which opens the way to the eventual identification of the illusive attractive compounds (D'Alessandro et al. 2009). Selection of plants with high release rates of such compounds could be an effective way to control pests in maize fields. In the process of identifying individual attractive compounds, the use of volatile extracts has an advantage over the use of intact plants or plant parts. With volatile extracts, it is possible to fractionate the odour blend, so that independent fractions and/or combinations of fractions could be tested for their attractiveness to insects in olfactometer bioassays (Colazza et al. 2004; Steiner et al. 2007; D'Alessandro et al. 2009). To use this methodology for the identification of plant-produced parasitoid attractants, appropriate starting material should be selected. The current study suggests that the use of headspace extracts obtained from teosintes may be more suited than headspace extracts obtained from maize for the identification of key parasitoid attractants, in particular, those of *C. marginiventris*.

In conclusion, we found evidence that there are ecologically relevant differences between the odours of modern maize and teosintes, possibly indicating a loss in maize's ability to attract certain natural enemies of herbivores. We propose to use the ancestors of maize, the teosintes, for the eventual identification of key signals that are involved in parasitoid attractiveness. The identification of these attractants will not only provide new insights into plant-mediated tritrophic interactions, but may also help in selecting or creating new maize varieties that are optimally compatible with biological control.

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picture in Online Resource 1 was made by Matthias Held and Fig. 1 was created by Thomas Degen (http://www.thomas-degen.ch).

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