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Variability in herbivore-induced odour emissions among maize cultivars and their wild ancestors (teosinte)

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Summary. Maize plants respond to caterpillar feeding with the release of relatively large amounts of specific volatiles, which are known to serve as cues for parasitoids to locate their host. Little is known about the genetic variability in such herbivore-induced plant signals and about how the emissions in cultivated plants compare to those of their wild relatives. For this reason we compared the total quantity and the qualitative composition of the odour blend among eleven maize cultivars and five wild *Zea* (Poaceae) species (teosinte), as well as among the offspring of eight *Zea mays mexicana* plants from a single population. Young plants were induced to release volatiles by mechanically damaging the leaves and applying oral secretions of *Spodoptera littoralis* (Lepidoptera: Noctuidae) caterpillars to the wounded sites. Volatiles were collected 7 h after treatment and subsequently analysed by gas chromatography. The total amounts of volatiles released were significantly different among maize cultivars as well as among the teosintes. Moreover, striking differences were found in the composition of the induced odour blends. Caryophyllene, for instance, was released by some, but not all varieties and teosintes, and the ratios among monoterpenes and sesquiterpenes varied considerably. The offspring of different mother plants of the *Z. m. mexicana* population showed some variation in the total amounts that they released, but the composition of the odour blend was very consistent within the population of this teosinte species. We discuss the ecological significance of these findings in terms of specificity and reliability of induced plant signals for parasitoids.

Key words. Induced plant volatiles – specificity – reliability – tritrophic interactions – *Zea mays* – maize – teosinte

Introduction

Odour emissions by plants in response to herbivory have been intensively studied for the past decade. This phenomenon has been demonstrated for several systems, mostly involving cultivated plants like Lima bean (Fabaceae), cabbage (Brassicaceae), cucumber (Cucurbitaceae), apple (Rosaceae), cotton (Malvaceae) and maize (Poaceae) (Dicke *et al.* 1990; Turlings *et al.* 1990, 1993a; Takabayashi *et al.* 1991; Agelopoulos & Keller 1994; Mattiacci *et al.* 1994; McCall *et al.* 1994; Pallini *et al.* 1997; Röse *et al.* 1997). For a variety of natural enemies of herbivores it has been found that they make use of these induced plants odours for long-range prey or host location (Dicke & Sabelis 1988; Turlings *et al.* 1990; Agelopoulos & Keller 1994; Takabayashi *et al.* 1995; Powell *et al.* 1998). This reliance on plant-provided cues is thought to be a consequence of the absence of detectable amounts of kairomones, cues that originate directly from the host (Tumlinson *et al.* 1993; Vet & Dicke 1992). Plant odours are considered to be less reliable than kairomones, because plant odours appear to provide little information on the identity of the herbivore that causes their release (Vet & Dicke 1992). Moreover, suitable hosts can occur on different plant species that all release their own odour blend (Turlings *et al.* 1993a). It appears that even within one species of plant the odours can vary considerably (Takabayashi *et al.* 1991; Turlings *et al.* 1998a).

Variability in induced plant odours complicates the reliance of parasitoids on these cues. One way of dealing with variability is through associative learning (Turlings *et al.* 1993b; Vet *et al.* 1995), which may allow parasitoids to learn which cues are most likely to lead them to suitable hosts at a particular time in a particular area. Moreover, recent studies suggest that plant odours alone carry specific information on the herbivores by which they are attacked. For example, predatory mites are able to distinguish between the odours of apple trees infested by two herbivores species (Sabelis & van de Baan 1983; Sabelis & Dicke 1985; Takabayashi *et al.* 1991). Guerrieri *et al.* (1999) showed that different aphid species elicit different odour emissions in bean plants and that the aphid parasitoid, *Aphidius ervi* (Hymenoptera: Braconidae: Aphidiinae), can use these differences to distinguish plants infested by its host, *Aphis pisum* (Homoptera: Aphididae), from those infested by a non-host, *Aphis fabae* (Homoptera: Aphididae). Similarly, De Moraes *et al.* (1998) found that the

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specialist parasitoid, *Cardiochiles nigriceps* (Hymenoptera: Braconidae), is more attracted by plants on which their specific host, *Heliothis virescens* (Lepidoptera: Noctuidae), has been feeding than by plants attacked by *Helicoverpa zea* (Lepidoptera: Noctuidae). These examples show that the induced signals emitted by plant under herbivore attack can vary depending on the insect species that feed on the plant and could therefore provide parasitoids and predators information on the suitability of the herbivore on the plants.

Differences in the intensity by which the odours are emitted are unlikely to provide specific information. Distinguishable differences would require that some volatiles are released in different proportions relative to each other, which appear to be what *C. nigriceps* is able to detect (De Moraes *et al.* 1998), or that the odour blends contain different volatiles substances, which may be what the aphid parasitoid uses (Du *et al.* 1998).

Considering that different plant species release entirely different odour blends and that even within one plant species there are clear differences among genotypes (Takabayashi *et al.* 1991; Turlings *et al.* 1998a), the possibility for parasitoids and predators to rely on specific cues seems therefore limited. Studies into the specificity of herbivore-induced plant signals should consider this intraspecific variability. The little information that is available on the extent of the variability comes from studies on cultivated plants (Takabayashi *et al.* 1991; Turlings *et al.* 1998a; Krips, 2000). For a better understanding of the ecological relevance and evolutionary history of herbivore-induced plant signalling, it is necessary to study these signals in wild systems. The only such study has been done with a naturalised cotton variety which was found to release much higher quantities of induced volatiles than cultivated varieties (Loughrin *et al.*, 1995).

The current study was conducted to obtain more information on the specificity and variation in the induced responses within the genus *Zea*, including several wild species. Odours from eleven cultivated varieties of maize were collected at different times after leaves were damaged and treated with the oral secretions of *Spodoptera littoralis* (Lepidoptera: Noctuidae) larvae. The same experiment was conducted with five species and subspecies of teosinte, the wild relatives of maize. The obtained variation in induced odour blends was compared to the variation within a population of the teosinte *Zea mays mexicana*. For this, we analysed the volatiles collected from plants grown from seed collected from eight individual plants in a Mexican population.

Materials and methods

Plants

Seed from eleven commercially available varieties of maize (*Zea mays mays* L.) were provided by UFA Semences, Bussigny (Switzerland), except for the varieties Byzance and Pactol, which were obtained from Novartis, St Sauveur (France). In all experiments the variety Delprim was used as a reference. The ten other cultivars were tested in two separate blocks. In an additional experiment, we tested five taxa of teosinte, *Zea perennis*, *Z. diploperennis*, *Z. luxurians*, *Z. mays mexicana*, and *Z. m. parviglumis*. Seeds of these species were provided by the USDA-ARS, North Central Regional Plant Introduction Station, Iowa State University, USA. Teosinte seed were first placed on moist filter paper in a 5.5 cm diameter Petri dish for germination. The same procedure was used for seed of eight individual plants of *Z. m. mexicana* race Chalco that had been collected in December 1998 from a small population near Texcoco, Mexico. To break dormancy, the seeds were placed at 4°C for a week before they were placed on moist filter paper to germinate. All seeds were eventually planted in pots (360 ml, 10 cm diameter, 7 cm high) filled with soil mixture composed of 80% of regular potting soil (Coop, Switzerland) and 20% of vermiculite (medium size, HK, Switzerland). Plants were kept in a climate chamber (Type 10′US/ + 5 DU-PI, Weiss Umwelttechnik GmbH, Switzerland) under the following conditions: 23°C ± 4°C, 60% ± 10% r. h., and 40000 lm/m^2 with a photoperiod of L16:D8. The plants were watered daily. After 10 days, at which age all cultivars carried three developed leaves with the fourth showing, the plants were used for experiment. The teosintes carried the same number of leaves, but the leaves were longer and thinner than those of cultivated plants.

Treatment of plants

Regurgitant used to elicit odour emission was collected from third and fourth instar *Spodoptera littoralis* larvae as described by Turlings *et al.* (1993a). The larvae were provided by Novartis Insect Control, Basle (Switzerland) and fed maize leaves for at least one day before regurgitant collection.

Maize seedlings were induced to emit volatile synomones by scratching 2 cm^2 of a leaf surface with a razor blade and applying 10 µl of *S. littoralis* regurgitant to the damaged site. We chose this easily standardised method rather than using actual larvae to avoid differential feeding damage, which may result in high variability in odour emissions (Gouinguené, unpubl. data). For all cultivated varieties and *Z. m. mexicana*, the second and third leaf were treated. Because of considerable differences in leaf size we decided to treat the third and fourth leaves of the other four teosintes. Treatments took placed during the dark period, 7 h before lights were turned on.

Collection and analysis of induced maize volatile

The volatile collection system has been described in detail by Turlings *et al.* (1998a). It basically consists of 6 vertically placed cylinders (9.5 cm inner diameter, 54 cm high). The aerial part of a plant was placed in a cylinder, while the pot with the subterranean part remained outside, separated from the shoot by a teflon disk consisting of two halves with a hole in the centre (Turlings *et al.* 1998a). Purified and humidified air was pushed into each cylinder at a rate of 1 l/min. Around the base of each cylinder, just above the teflon disk, 8 openings served as ports that could hold the collection traps. Three ports were used during an experiment; the others were sealed. Collection traps consisted of 6 mm diameter and 7 cm long glass tube that held 25 mg of Super Q adsorbent (80–100 mesh, Alltech, Deerfield, Illinois, USA) (Heath & Manukian 1994). During the collections, air was pulled through a trap at a rate of 0.8 l/min, while the rest of the air vented out through the hole in the bottom, thus preventing outside, impure air from entering. The automated part of the collection system (Analytical Research System, Gainesville, Florida, USA) controlled the flow through the traps and made it possible to switch this flow from one trap to another. The climate chamber (CMP4030, CONVIRON, Winnipeg, Canada) in which the collection cylinders were housed was kept at 17.5°C, due to the irradiation heat, the temperature inside the cylinders was 23 ± 3°C. During the light cycle, light intensity was about 20000 lm/m^2.

Immediately when lights went on, *i.e.* 7 h after treatment, odours were collected during three consecutive 3-h periods. In most cases, the maximum volatile production occurred during the second collection period, therefore collection was only done during this period in the experiment with the *Z. m. mexicana* plants from the Texcoco population.

Traps were extracted with 150 µl of methylene chloride (Lichrosolv., Merck, Switzerland) and 200 ng of n-octane and nonyl acetate (Sigma, Switzerland) in 10 µl methylene chloride were added to the samples as internal standards.

Analyses were done with a Hewlett Packard HP 6890 series gas chromatograph equipped with an automated on-column injection system (HP G1513 A) and a flame ionisation detector. Of each sample a 3 µl aliquot was injected onto an apolar EC-1 capillary column (30 m, 0.25 mm. i.d., 0.25 µm film thickness, Alltech Associates, Inc, USA) preceded by a deactivated retention gap (10 m, 0.25 mm i.d., Connex, USA) and a deactivated pre-column (30 cm, 0.530 mm i.d., Connex, USA). Helium (24 cm/s) was used as carrier gas. Following injection, the column temperature was maintained at 50°C for 3 min, increased to 230°C at 8°C/min and held at 230°C for 9.5 min. The detector signal was processed with HP GC Chemstation software. Tentative identification of compounds was based on comparison of retention times with analyses from previous studies (Turlings *et al.* 1998a). These identities were confirmed with spectra from the Wiley library after mass spectrometry analyses of 3 selected samples with the above column and temperature program in a Hewlett-Packard 5973 mass selective detector (transfer line 230°C, source 230°C, quadrupole 150°C, ionisation potential 70 eV, scan range 50–400 amu).

Statistical analyses

The amounts of the eighteen dominating compounds in the collections were determined based on their relative peak areas and those of the internal standards. The total amounts of these compounds emitted during the three collection periods (9 h) were summed. Differences between varieties and teosinte taxa were determined using one way analysis of variance. Each experimental block was analysed separately. The Student-Newman-Keuls test was performed for multiple comparisons. To comply with ANOVA assumptions, all data were ln-transformed. The same analysis was performed for each compound to check for differences between varieties and teosinte.

Results

Quantitative differences

The amount of volatiles varied with time after plant treatment (Fig. 1). The maximum emission occurred during the second collection period, 10 to 13 h after treatment, except for the varieties Byzance and Pactol, and the teosintes, *Z. m. parviglumis* and *Z. luxurians*, which released more during the third collection period, 13 to 16 h after treatment (Fig. 1).

The total amount of induced volatiles emitted during the 9 h of collection varied considerably among the different maize genotypes (Fig. 2). For example, the variety Pactol emitted 3 times more than the variety Byzance (Fig. 2A). Even more dramatic were the differences among the varieties in the second block (Fig. 2B). The average amount released by the variety Husar was 8 times and 6 times higher than for the varieties Challenger and Best, respectively. Significant differences were also found in the total amount of odour emitted among the teosinte. For example, *Z. m. parviglumis* releases 8 times as much as *Z. perennis* (Fig. 2C). The wild relatives of maize emitted lower amount of odour compared to Delprim, except for the subspecies *Z. m. parviglumis*, which emitted more than this reference variety.

The considerable differences in total amounts emitted by Delprim for the different blocks may be due to differences in light quality in the climate chambers over time. The experimental blocks were conducted several months apart.

Qualitative differences

Differences were also found in the quality of the odour blends. The proportion of the principle compounds in the blends appeared characteristic for each genotype (Fig. 3). The ratio between the two terpenoids, linalool and (*E*)-4,8-dimethyl-1,3,7-nonatriene was different for several varieties. For example, Delprim emitted more linalool than (*E*)-4,8-dimethyl-1,3,7-nonatriene, but the reverse was found for the variety Byzance and *Z. luxurians*. Also, the amount of the aromatic compound, indole, varied with variety. Byzance was the only variety in which indole was the major compound, representing about 40% of total emission. Differences in compound ratio was most dramatic among the three sesquiterpenes, β-caryophyllene, (*E*)-α-bergamotene and (*E*)-β-farnesene, which together accounted for 22 to 84% of the total emitted by the different genotypes. All the varieties released these three sesquiterpenes, except Pactol, which did not emit β-caryophyllene.

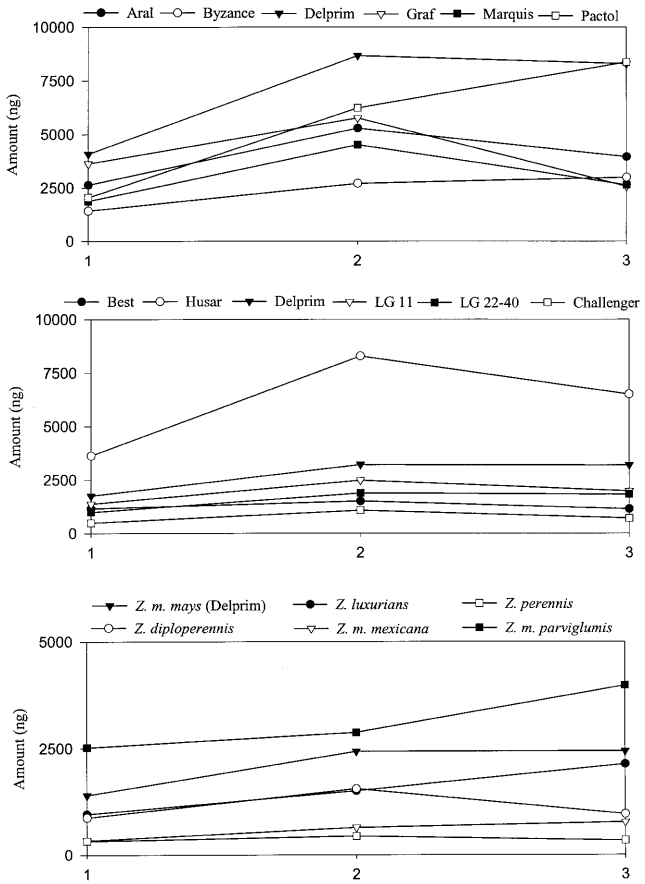

Fig. 1 Total amount of induced volatile compounds emitted by maize cultivars and teosinte after damaging and treating them with caterpillar regurgitant ($N = 6$) (period 1: from 7 to 10 h after treatment; period 2: from 10 to 13 h after treatment; period 3: from 13 to 16 h after treatment)

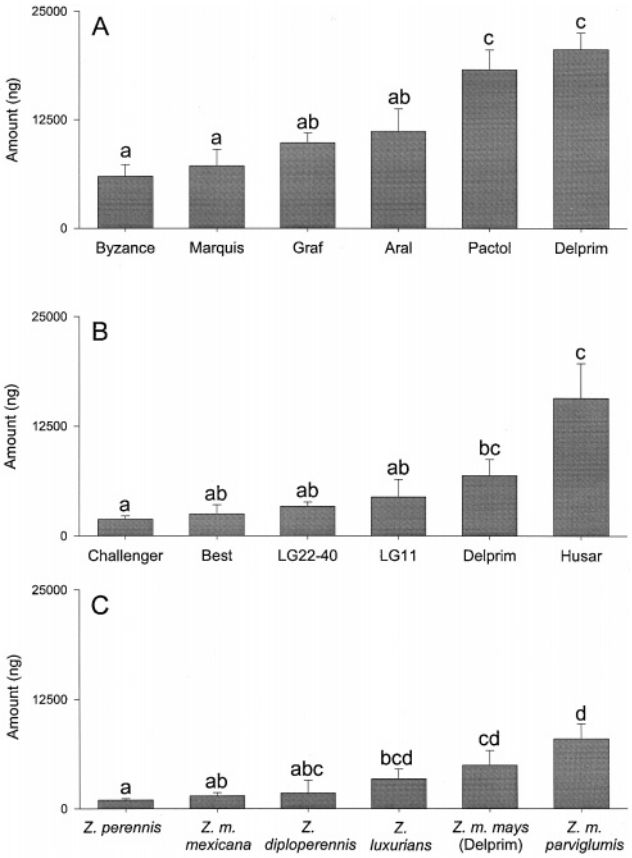

Fig. 2 Total amount of induced volatiles emitted by different maize varieties (**A, B**) and teosintes (**C**) in ng summed for three collection periods (9 h). Statistical analysis were performed on ln transformed data and the graphs are based on the back transformation of the mean ($\pm$SE, $N = 6$). Letters above each bar indicate significant differences after Student-Newman-Keuls post hoc test for $\alpha = 0.05$

Among the teosintes, *Z. diploperennis* and *Z. m. mexicana* released very small quantities of β-caryophyllene (respectively 0.63% and 0.92% of the total blend).

Byzance, Graf and LG22-40 were the varieties in which the sum of the three sesquiterpenes made up less than 30%. In the species *Z. diploperennis* and *Z. m. mexicana* these compounds dominated and represented 74% and 84% of the entire blend, respectively.

Variation within the Z. m. mexicana *population*

The total amount of induced odour emitted by the offspring of eight different *Z. m. mexicana* mother plants is shown in Figure 4. Differences between families of this small population were not significant, despite a clear trend that some plants emitted lower amount of induced odour than others did. The composition of the induced odour was very similar from one plant to another, independent of the mother plant (Fig. 5). Hence, variability within the *Z. m. mexicana* population appears small.

Discussion

We found substantial variability in induced volatile signals among maize cultivars, as well as among wild relatives of maize, both in terms of total amount (quantity) and quality. Some genotypes released up to 8 times more than others did. Differences in quality of induced odour blends refer to differences in identity of the compounds within a blend and to differences in ratios among these compounds. Such differences were most apparent for the sesquiterpenes, which showed considerable variability in ratios. As we previously found (Turlings *et al.* 1998a), β-caryophyllene was not emitted by all genotypes. The comparison of the three collection periods (Fig. 1) indicated that maize genotypes also vary in the timing of their response.

The range of variation in the amounts of volatiles emitted by the teosintes is very comparable to the one found for the cultivars. Concerning the quality of the odour blend, the volatile profile appears largely preserved in maize. All compounds in wild relatives can also be found in cultivated varieties. The only other study that compared the odour emissions between cultivars and a wild form was by Loughrin *et al.* (1995) who compared several cultivated cotton (Malvaceae) varieties with a naturalised variety. The wild version released considerably more volatiles. This was not the case in our study, which indicates that the breeding process did not significantly effect this trait in maize. This is contrary to the expectation that breeding for increased yield and palatability will result in a decrease of secondary defence substances in domesticated plants (Benrey *et al.*, 1998). Interestingly, *Z. m. parviglumis*, which is considered the closest relative to cultivated maize (Doebley & Wang 1997; Kellogg 1997), produced more than the other teosintes.

Many examples exist on the differences in emission of induced odour by different plant species, on how different herbivore types can affect the induced odour blend, and how natural enemies discriminate between plants infested by different herbivore types (Dicke & Vet 1999). Indeed, recent studies suggest that plants provide specific information on the identity of the herbivore by which they are attacked. For instance, Dicke & Takabayashi (1991) found that mite-induced synomones can be specific for both the herbivore species and the plant species. In fact, predatory mites are able to distinguish between apple foliage infested by different species of spider mites (Sabelis & van de Baan 1983; Dicke & Takabayashi 1991). Similarly, the aphid parasitoid *Aphidius ervi* can distinguish between plant infested by its host aphid and plant infested by a non-host aphid. This difference in the attraction of the parasitoid is speculated to be due to a compound (6-methyl-5-hepten-2-one), which was only detected in the odour blend of plants attacked by the host (Du *et al.* 1998; Guerrieri *et al.* 1999). As pointed out by Du *et al.* (1998), the study was done with only one genotype of one plant species, but the host aphid can feed on several other plant species. It would be interesting to

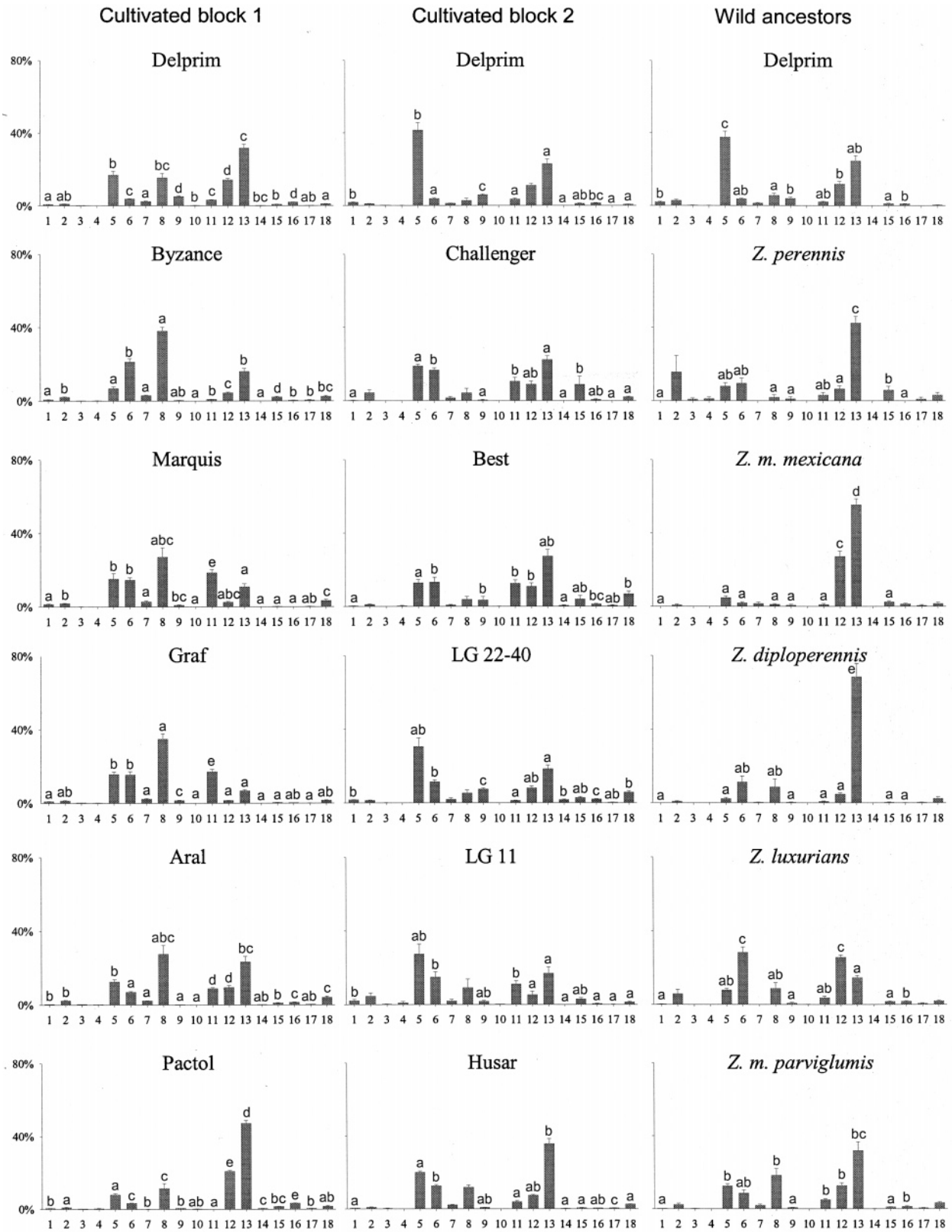

Fig. 3 Relative amount ($\pm$ SE) of the 18 main compounds (% of the total amount of induced odour) emitted by cultivated maize varieties and 5 species of teosinte. One-way anova was performed for each compound and followed by Student-Newman-Keuls test. Letters above the bars represents significant differences in the emission of a particular compound within each of the three columns (experimental blocks). (**1**) β-myrcene; (**2**) (*Z*)-3-hexen-1-yl acetate; (**3**) hexyl acetate; (**4**) (*Z*)-β-ocimene; (**5**) linalool; (**6**) (*E*)-4,8-dimethyl-1,3,7-nonatriene; (**7**) phenethyl acetate; (**8**) indole; (**9**) geranyl acetate; (**10**) unknown; (**11**) β-caryophyllene; (**12**) (*E*)-α-bergamotene; (**13**) (*E*)-β-farnesene; (**14**) α-humulene; (**15**) unknown sesquiterpene; (**16**) (*E*,*E*)-α-farnesene; (**17**) (*E*)-nerolidol; (**18**) (3*E*,7*E*)-4,8,12-trimethyl-1,3,7,11-tridecatetraene

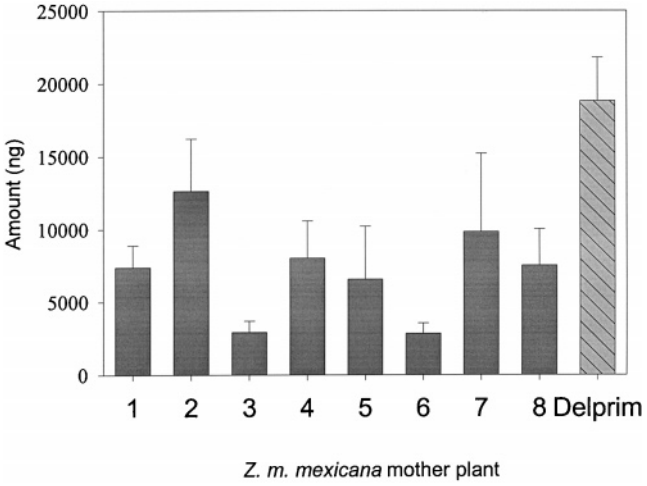

Fig. 4 Total amount in ng of volatiles emitted by the offspring of eight *Z. m. mexicana* plants and Delprim. Statistical analysis were performed on ln transformed data and the graphs are based on the back transformation of the mean ($\pm$SE, $N = 8$). No significant differences were found among the teosinte ($F_{7,1.080} = 1.510$, $P = 0.208$)

see if *A. ervi* is able to distinguish among hosts and non-hosts on different plants and if the same compound or compounds are involved.

De Moraes *et al.* (1998) showed that the specialist endoparasitoid *Cardiochiles nigriceps* is more attracted to tobacco (Solanaceae) attacked by its host (*Heliothis virenscens*) than by tobacco attacked by a related non-host (*Heliothis zea).* Collections of the odour emitted by tobacco attacked by either herbivore revealed consistent differences in the ratios in which several compounds were released (De Moraes *et al.* 1998).

The induced odour emitted by plants may also give information on the host stage that is feeding on a plant. Takabayashi *et al.* (1995) found that late instar larvae of *Pseudatelia separata* (Lepidoptera: Noctuidae) do not induce an emission of volatiles in maize plants, while plants attacked by early stages of herbivore release large amounts of induced odour and are very attractive to the specialist parasitoid, *Cotesia kariyai* (Hymenoptera: Braconidae).

It seems that signal specificity requires that there is little intraspecific variability in how plants respond to a

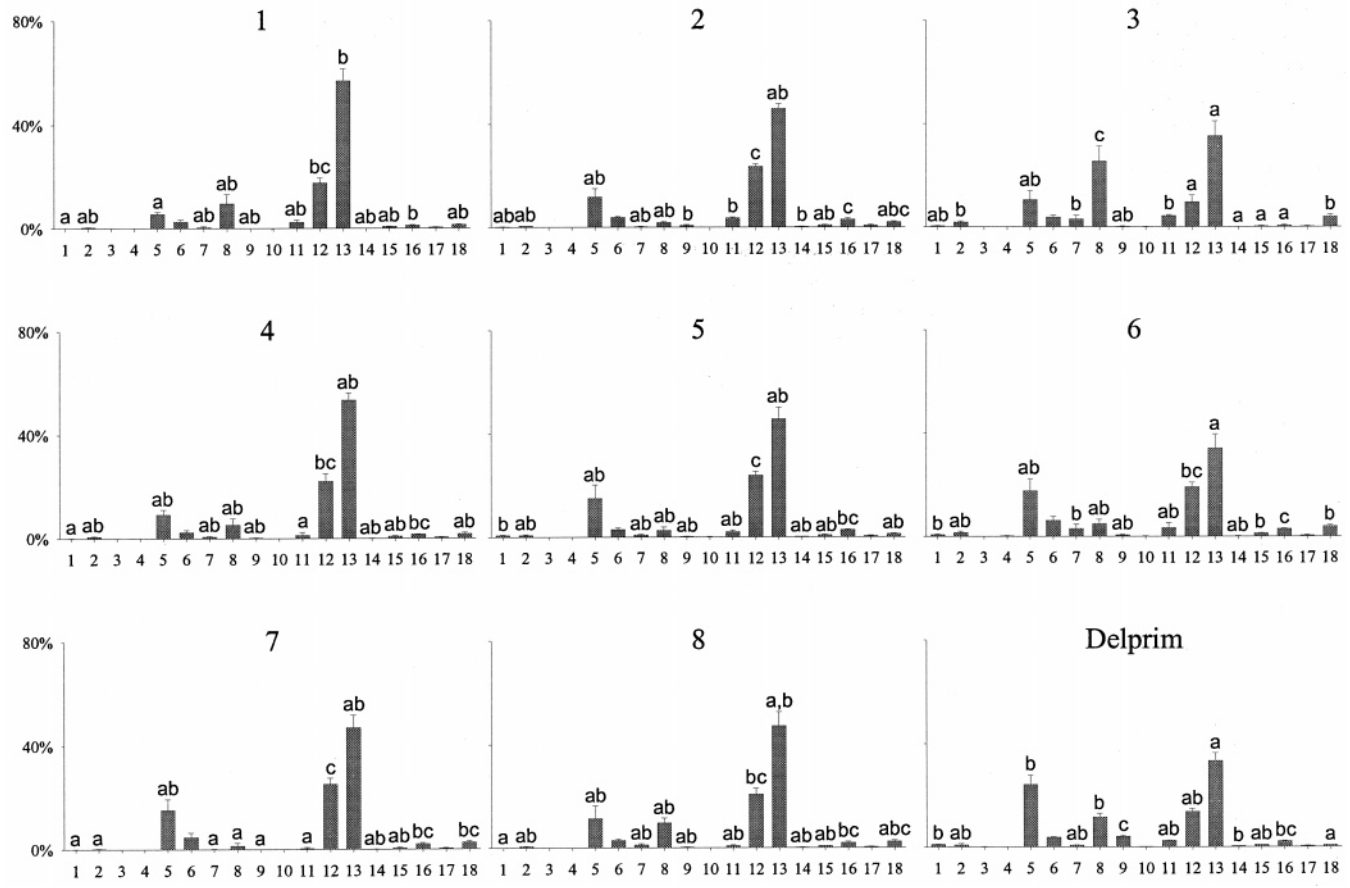

Fig. 5 Relative amount of the main compounds (% of the total amount of induced odour $\pm$SE) emitted by the offspring ($N = 8$) of eight *Z. m. mexicana* mother plants obtained from a single population. One-way anova was performed for each compound and followed by Student-Newman-Keuls test in case of significant differences, which are indicated by letters above bars. (**1**) β-myrcene; (**2**) (*Z*)-3-hexen-1-yl acetate; (**3**) hexyl acetate; (**4**) (*Z*)-β-ocimene; (**5**) linalool; (**6**) (3*E*)-4,8-dimethyl-1,3,7-nonatriene; (**7**) phenethyl acetate; (**8**) indole; (**9**) geranyl acetate; (**10**) unknown; (**11**) β-caryophyllene; (**12**) (*E*)-α-bergamotene; (**13**) (*E*)-β-farnesene; (**14**) α-humulene; (**15**) unknown sesquiterpene; (**16**) (*E,E*)-α-farnesene/β-bisabolene; (**17**) (*E*)-nerolidol; (**18**) (3*E*, 7*E*)-4,8,12-trimethyl-1,3,7,11-tridecatetraene. Due to poor separation, peak 16 often contained two compounds that we counted as one in our calculations

particular herbivore. The few studies that compare induced odour blends emitted by different cultivars of the same plant species attacked by the same herbivores indicate considerable variation. For example, the odour induced by the mite *Tetranicus urticae* (Acari: Tetranychidae) varies considerably between two apple cultivars and these differences are considerably larger than differences found for one apple cultivar infested by two different mites species (Takabayashi *et al*. 1991). Krips (2000) compared the odour emissions in four gerbera (Asteraceae) cultivars after spider mite attack and also found large differences in terpenoid emissions. For instance, the variety Sirtaki does not release (*E*)-β-farnesene while it is present in the odour blend of the other varieties. We previously showed a distinct difference in the induced odour blend of two maize cultivars, LG11 and Iona sweet corn (Turlings *et al*. 1998a). β-Caryophyllene is not released by Ioana sweet corn, as was found here for the variety Pactol.

This comparison of several cultivars has provided additional information on the range of variation between genotypes of the same species. Within the genus *Zea*, variation can be quite dramatic, both in overall quantity as well as in the composition of the induced odour blend. Such genetic variability is likely to be larger than what different herbivores contribute to variation. Yet, herbivores may cause detectable differences through different feeding habits (Turlings *et al*. 1998b) or through different elicitors that come in contact with leaf tissue while they are feeding (Hopke *et al*. 1994). The reliability of induced plant signals for the third trophic level remains unclear. As pointed out by Dicke (1999), chemical analyses provide limited information in this respect because of the detection limits of the techniques that we employ. Behavioural assays with parasitoids will have to be carried out to determine what information they exactly obtain from the different odour blends.

The results presented here reveal considerable variation in induced odours among maize genotypes. Parasitoids that will have to deal with this variability may benefit from being flexible in their responses. To make optimal use of the cues that are reliably associated with hosts in a given plant population they probably rely on their ability to learn (Vet & Groenewold 1990; Turlings *et al*. 1993b; Vet *et al*. 1995). The observed variability also suggests that maize genotypes will vary in their attractiveness to natural enemies of herbivores. If so, this could be exploited in crop protection by selecting and breeding crop plants that release compounds that are particularly attractive to biological control agents. In maize, there appears to be sufficient genetic variation to facilitate such efforts. An important next step is to determine which of the volatiles are essential in the foraging behaviour of beneficial insects.

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