Published in Planta 207, issue 1, 146-152, 1998
which should be used for any reference to this work

Timing of induced volatile emissions in maize seedlings

Ted C.J. Turlings[1*], Urs B. Lengwiler[1], Marco L. Bernasconi[1], Daniel Wechsler[2]

[1]Institute of Plant Sciences/Applied Entomology, Swiss Federal Institute of Technology (ETH), CH-8092 Zurich, Switzerland
[2]Institute of Food Sciences, Swiss Federal Institute of Technology (ETH), CH-8092 Zurich, Switzerland

Abstract. Maize (*Zea mays* L.) releases specific volatiles in response to herbivory by caterpillars. These volatiles are known to serve as cues for parasitic wasps to locate the herbivores. In the present study the exact time of volatile emission after simulated herbivory (mechanical damage and treatment with caterpillar regurgitant) was measured for seedlings of the cultivars "Ioana Sweet Corn" and "LG11". Odours were collected every 0.5 h for a total of 12 h. Typical "green leaf odours", (Z)-3-hexenal, (*E*)-2-hexenal, (Z)-hexen-1-o1, and (Z)-3-hexen-1-yl acetate, were emitted immediately upon damage and their amounts dropped rapidly after the first collections. Several of the induced compounds were released within 2 h after treatment, while others (mainly sesquiterpenoids) started to be released after 4 h. The LG11 seedlings emitted several compounds (e.g. β-myrcene, (Z)-β-ocimene, benzyl acetate, β-caryophyllene, (*E*,*E*)-α-farnesene) that were not detected for Ioana. (*E*,*E*)-α-farnesene was continuously emitted by LG11 seedlings, even by undamaged plants. Timing of the release of volatile compounds that the two varieties had in common did not differ significantly, with the exception of indole for which the peak production was considerably earlier for LG11. These findings are discussed in the context of biosynthetic pathways and mechanisms involved in induced emissions of plant volatiles and the exploitation of the resulting odour by parasitoids and predators of herbivores.

**Present address*: University of Neuchâtel, Institute of Zoology, Lab. of Animal Ecology and Entomology, rue Émile-Argand 11, CH-2007 Neuchâtel, Switzerland

Correspondence to: T.C.J. Turlings;
E-mail: ted.turlings@zool.unine.ch; Fax: 41 (32) 7183001

Key words: Induced defence – Parasitoid – Plant-insect interactions – Semiochemicals – Volatiles – *Zea mays*

Introduction

Plants commonly respond to damage with the production and/or release of specific chemicals (Tallamy and Raupp 1991; Baldwin 1994). Timing of response can vary considerably. In some plants, the chemical changes start within minutes after damage, while in other plants the effects are observed only after years (Baldwin 1994). The function of the induced production of plant secondary compounds remains a topic of discussion and disagreement (e.g. Rhoades 1979; Edwards and Wratten 1985; Schultz 1988; Faeth 1992, 1994; Karban 1992a,b). It is, however, generally assumed that at least some of the chemicals serve in the defence against the plant's attackers.

Several substances produced by the plants in response to herbivory are volatile and some are emitted systemically throughout the plant (Turlings and Tumlinson 1992; Röse et al. 1996). Immediately upon damage to their leaves, plants typically release a blend of "green leafy" compounds. These lipoxygenase products (six-carbon aldehydes, alcohols, and acetates) "bleed" from ruptured plant cells. If the damage ceases, the emission of these compounds drops rapidly and will stop within hours (Loughrin et al. 1994; Turlings et al. 1995). Similar emission patterns are found for volatile compounds that are constitutively present in plants. Cotton plants, for instance, possess glands in which constitutive defence volatiles are stored. When these glands are ruptured the volatiles (mainly terpenoids) are emitted instantaneously and their emission drops soon after the attack on the plant stops (Loughrin et al. 1994; McCall et al. 1994; Röse et al. 1996).

In contrast to green-leaf volatiles and constitutive volatiles, plants also display an induced release of volatiles, specifically in response to herbivory (Dicke et al. 1990; Turlings et al. 1990; Röse et al. 1996). Induced releases of plant volatiles have received attention because they are used by predators (Dicke and Sabelis 1988; Dicke et al. 1990) and parasitic wasps (Turlings et al. 1990, 1995; McCall et al. 1993; Steinberg et al. 1993; Agelopoulos and Keller 1994) to locate herbivores, which they attack. The release of these compounds is the result of the induction of chemical processes (Paré and Tumlinson 1996, 1997b) and it takes some time after initial damage before the emissions are observed. The release is systemic; even undamaged leaves of injured plants will release these volatiles in, for instance, maize (Turlings and Tumlinson 1992) and cotton (Röse et al. 1996). In maize the production of volatiles is triggered by an elicitor that is present in the regurgitant of caterpillars (Turlings et al. 1993a). An elicitor from the beet armyworm was recently identified by Alborn et al. (1997) as volicitin, a conjugate of 17-hydroxy linolenic acid and glutamine. Induction of the volatile emission in maize specifically occurs in plants that are fed upon by caterpillars or treated with this elicitor, and does not occur, or barely occurs, in plants that are merely mechanically damaged (Turlings et al. 1990, 1993a; Alborn et al. 1997). Similar reactions in plants may be elicited by β-glucosidase in caterpillar regurgitant (Mattiacci et al. 1995), jasmonic acid, and the pathogen-derived amino acid conjugate coronatin (Boland et al. 1995).

Although we know that maize responds within hours (Turlings and Tumlinson 1992), the exact moment of the plant's emissions is not known. For the interactions with natural enemies of herbivores, a rapid response of the plant seems advantageous. In the current study an automated volatile-collection apparatus was used to precisely monitor the volatile emissions of maize seedlings over a 12-h period after simulated caterpillar damage. Two maize cultivars that are known to emit qualitatively different substances were tested and they showed a rapid response with distinct differences in timing of emission for different groups of compounds.

Materials and methods

Maize seedlings. Seeds of the maize (*Zea mays* L.) cultivars "Ioana Sweet Corn" (USDA-ARS, Tifton Ga., USA) and "LG11" (Fenaco, Winterthur, Switzerland) were individually planted in regular potting soil (Triohum, Substrat 1; Samen-Mauser, Winterthur, Switzerland) in 7 cm (diam.) × 6 cm (deep) plastic pots. The plants were kept in a climate chamber at 25 °C, 70% relative humidity, and 16:8 light:dark regime (lights on at 6 a.m.). The light intensity for the plants was 25,000 lux (Sylvania F96T12/CW/VHO) during the photophase. The seedlings were used for experiments 9–10 d after planting when they carried three leaves and the fourth leaf had just started to show.

Caterpillar regurgitant. Caterpillars (*Spodoptera littoralis*) were provided by Ciba (Novartis) Pest Control (Basle, Switzerland). The insects were kept on a wheatgerm-based artificial diet at room temperature. Regurgitant of third- and fourth-instar larvae was collected as described by Turlings et al. (1993a). The collected material was centrifuged and the supernatant was filtered through a 0.22 μm filter to remove large particles and micro-organisms, and subsequently stored at 3 °C until it was used for the treatment of plants.

Treatment of the plants. In all experiments, plants were either left undamaged, or the undersides of the three oldest leaves were scratched with a scalpel and treated with caterpillar regurgitant. Each scratched area was approximately 2 cm^2 and 5 μl regurgitant was applied to it. In all cases the plants were treated at 9 a.m. Per test we used three plants of the same cultivar, one was left undamaged and the other two were treated. Immediately after treatment each plant was carefully placed inside the volatile-collection system (see below). For both cultivars the experiment was repeated four times. Thus, the odours were collected from eight damaged and four undamaged plants of each cultivar.

Volatile-collection system. Volatiles emitted by individual maize seedlings were collected in a system modified after Heath and Manukian (1994). Air was first pushed through a bubbler to humidify, a flowmeter (Aalborg Instruments & Controls Inc., Monsey N.Y., USA) to measure and regulate the air flow, and a charcoal filter to purify the air. The moist and pure air then entered a glass cylinder (10 cm diam, 50 cm high) at 800 $ml \cdot min^{-1}$. To create a laminar flow, the air was forced through a glass frit at the top of the cylinder (Fig. 1). The air then passed over a plant that was placed in the cylinder through the open bottom. A Teflon disk was placed against the bottom of the cylinder. The disk consisted of two halves; a "guillotine-like" metal plate was attached to one half and this could be pushed into a groove in the other half (Fig. 1). A hole of 1 cm diameter was left in the centre of the disk for the stem of the plant. The two halves were pushed together around the lower part of the plant's stem, which left most of the plant and all of its leaves inside the cylinder, while the pot remained outside. This ensured that only odours from the plant were present in the cylinder. The Teflon disk had a 1-cm-wide and 5-mm-deep grove, which precisely fitted the widened base of the glass cylinder. Approximately 2.5 cm above the base of the cylinder, eight glass ports with screw caps and Teflon-sealed O-rings allowed for the attachment of collection traps. The collection traps were glass tubes (8 cm long, 6 mm diam.) that contained 30 mg of 80/100 mesh Super Q adsorbent (Altech Assoc., Deerfield, Ill., USA [see Heath and Manukian (1992) for details on the collection traps]).

The traps were connected through the O-rings with their tips only a few millimetres away from the stem of the plant. Outside the cylinder the traps were attached to Tygon tubing connected to an automated flow controller (Analytical Research Systems, Gainesville, Fla., USA). The flow controller switched a vacuum flow from one collection trap to the next every 30 min. This ensured that each of the eight traps attached to a collection cylinder collected odours at its own designated time. Filters that had collected odours were replaced every 2–3 h. Air was pulled through a trap at a rate of 600 $ml \cdot min^{-1}$. By pulling out less (75%) than went into the cylinder, we ensured that the system was continuously purged through the hole in the centre of the Teflon disk and that no outside (dirty) air would enter the system. Collections of the volatiles started immediately after the plants were damaged at 9:00 a.m. (3 h after lights on). Every 0.5 h the vacuum flow was switched to a new filter for a total period of 12 h (from 9 a.m. until 9 p.m., 24 collections per plant).

On the day of an experiment, we collected from two treated and one healthy plant of a particular cultivar. In total we collected from eight treated plants and four healthy plants of each cultivar (576 collections).

Analysis of the volatiles. After removing the traps from the volatile-collection system, they were extracted with 150 μl methylene chloride and two internal standards were added (200 ng of

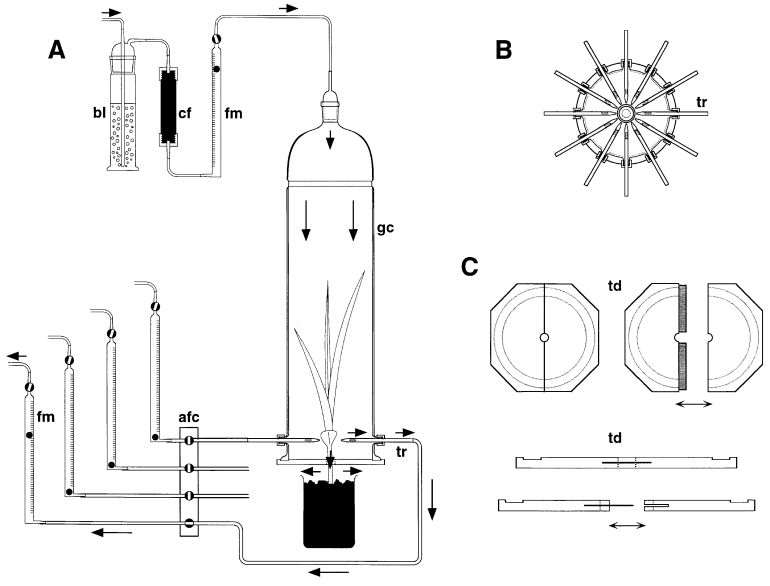

Fig. 1A–C. Apparatus for collection of volatiles. The system is based on one designed by Heath and Manukian (1994). **A** Air is first passed through a bubbler (*bl*) for humidification, a charcoal filter (*cf*) for purification, and a flowmeter (*fm*). The air enters the glass collection sleeve (*gc*) from the top and passes over the plant inside the sleeve. Volatile molecules emanating from the plant are carried by the air, of which 75% is pulled through one of the Super Q traps (*tr*) connected to the lower part of the sleeve. The remainder of the air is vented out through the central hole of the Teflon disk (*td*) that closes off the bottom of the glass sleeve an automated flow controller (*afc*) switches the vaccum flow from one trap to another at set times. **B** Arrangement of Super Q traps (*tr*). **C** Details of Teflon disk (*td*). See text for further details

n-octane and nonyl-acetate in 20 µl methylene chloride). Of each extract, 2 µl was analysed on an HP1 (cross-linked methyl silicone; Hewlett Packard) column (30 m × 0.25 mm i.d., 0.25-µm film) preceded by a deactivated retention gap (5 m × 0.25 mm i.d.). The Hewlett Packard model 5890 gas chromatograph (GC) was equipped with an on-column injector system and a flame ionisation detector. Helium at 21 cm · s^{-1} was used as a carrier gas. Following injection, column temperature was maintained at 40 °C for 4 min and then programmed at 5 °C · min^{-1} to 200 °C. Data were collected with Hewlett-Packard ChemStation software and the detected volatiles were quantified based on comparison of their peak areas with those of the internal standards.

For identification of the different compounds, selected samples were also analysed by GC-MS, using a Fisons GC 8065 gas chromatograph (Carlo Erba, Milan, Italy) coupled to a model SSQ 710 mass spectrometer (Finnigan MAT, San Jose, Calif., USA). For the gas-chromatographic separation the same HP-1 column was used with helium (25 cm · s^{-1}) as a carrier gas. The injector was held at 220 °C, employing a splitless injection of 15 s. The temperature program was: 40 °C for 5 min, increasing by 7 °C · min^{-1} up to 200 °C. The MS was used in the electron-impact mode (70 eV). For data analysis, ICIS 7.0 software (Finnigan MAT) was used, including the mass-spectra library NIST (National Technical Information Services, Springfield Virg., USA). Library matches and spectra interpretations revealed candidate compounds. Confirmations of identities were based on retention times and mass spectra of purchased synthetics which were analysed in an identical manner to the natural volatiles.

Results

During the first hour after damage, both Ioana and LG11 released large amounts of the green-leaf compounds, (Z)-3-hexenal, (*E*)-2-hexenal, (Z)-3-hexen-1-ol, (*E*)-2-hexen-1-ol, and (Z)-3-hexen-1-yl acetate (Figs. 2,3). All other compounds were absent at this early stage after treatment with the exception of *E*,*E*-α-farnesene, which was only released by LG11, even by undamaged plants. This is the first time that we have observed that healthy, undamaged maize plants emit detectable and consistent amounts of a particular substance. Occasionally, however, we detected linalool from undamaged plants of both cultivars. During the following 12 h the undamaged plants did not release any additional compounds, but the damaged plants initiated the release of a series of compounds at different time intervals.

Less than 2 h after treatment of the plants, linalool, (3*E*)-4,8-dimethyl-1,3,7-nonatriene, indole, and (3*E*, 7*E*)-4,8,12-trimethyl-1,3,7,11-tridecatetraene were emitted by both cultivars. It took 4–5 h before the other compounds that the two cultivars had in common were detected. At this point the odour blend emitted by both Ioana and LG11 included α-bergamotene, (*E*)-β-farnesene, and nerolidol (Fig. 2A). LG11 also released β-caryophyllene, which was detected much earlier than the others sesquiterpenes (Fig. 2B). Further compounds emitted by LG11 were (Z)-β-ocimene, benzyl acetate, and phenethyl acetate. Occasionally, we found trace amounts of some compounds that we identified from LG11 in a previous study (Turlings et al. 1998). These were β-myrcene, 1-hexyl acetate, methyl salicylate, methyl anthranilate, and geranyl acetate.

Based on the timing of their emissions the compounds that were detected for both cultivars can be roughly divided into four groups: (1) the green-leaf volatiles, (2) the early terpenoids, (3) indole and (4) the later terpenoids. Fig. 3 shows the emission over time of four compounds that are representative of these groups. The patterns of release are similar for the two maize cultivars. Only the peak production of indole is much earlier for LG11 than for Ioana. Overall, the amounts released by LG11 were somewhat higher than for Ioana.

Discussion

From our results we can conclude that induced emissions of volatiles in maize occur rapidly after initial damage. In the context of interactions with insects this rapid reaction could serve the plants well. It is known that the odours are highly attractive to parasitic wasps

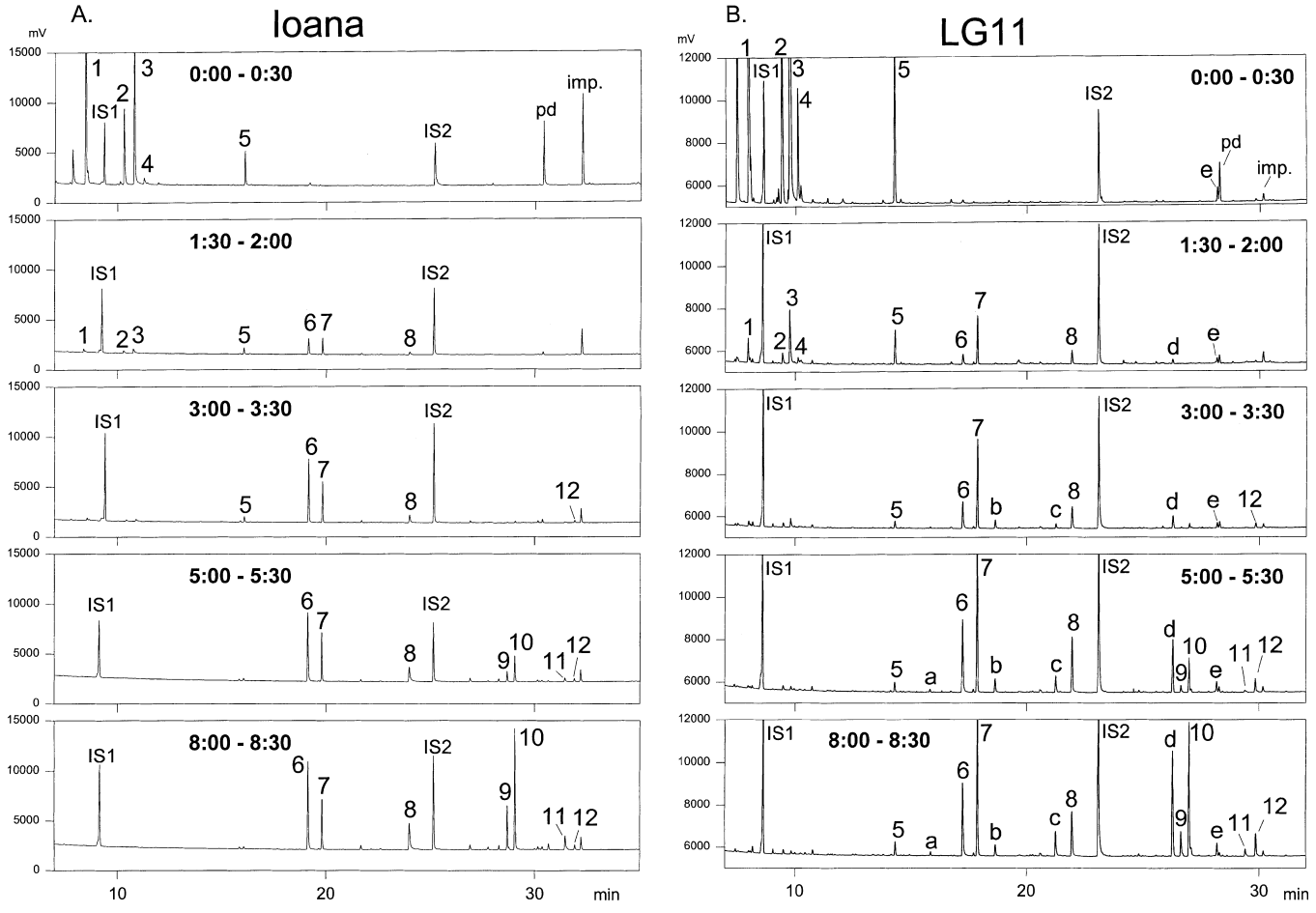

Fig. 2A–B. Chromatographic profiles of odours collected from seedlings of the maize cultivars Ioana (**A**) and LG11 (**B**) at different times (indicated) after damage and treatment with caterpillar regurgitant. The peaks with numbers represent compounds that were emitted by both genotypes. They are: *1*, (Z)-3-hexenal; *2*, (*E*)-2-hexenal; *3*, (Z)-3-hexen-1-o1; *4*, (*E*)-2-hexen-1-ol; *5*, (Z)-3-hexen-1-yl acetate; *6*, linalool; *7*, (*3E*)-4,8-dimethyl-1,3,7-nonatriene; *8*, indole; *9*, (*E*)-α-bergamotene; *10*, *E*-β-farnesene; *11*, (*E*)-nerolidol; 12, (*3E*, *7E*)-4,8,12-trimethyl-1,3,7,11-tridecatetraene. The letters mark the compounds that were only detected for LG11: *a*, (Z)-β-ocimene; *b*, benzyl acetate; *c*, phenethyl acetate; *d*, β-caryophyllene; *e*, (*E,E*)-α-farnesene. Two remaining volatiles did not originate from the plants; pentadecane (*pd*) was released from the regurgitant that was used to treat the plants and *imp*. represents an impurity in the air. IS1 and IS2 are the internal standards *n*-octane and *n*-nonyl-acetate

(Turlings et al. 1990, 1995) and probably also other natural enemies of the caterpillars. The fact that the maize plant responds so fast suggests that it may be able to attract these and other natural enemies long before the herbivore can do substantial damage. This would support the notion that one of the functions of the induced volatiles is to defend the plant indirectly by attracting arthropods that eliminate herbivores (Dicke and Sabelis 1988; Dicke et al. 1990; Turlings et al. 1995).

Paré and Tumlinson (1996, 1997b) categorised volatiles emitted upon herbivore-inflicted damage into three basic groups. First there are the green-leaf volatiles, (Z)-3-hexenal, (*E*)-2-hexenal, (Z)-3-hexen-1-ol, (*E*)-2-hexen-1-ol, and (Z)-3-hexen-1-yl acetate, which are products of the fatty acid/lipoxygenase pathway. They are the result of the oxidation of linolenic acid and subsequent transformations into (Z)-3-hexenal, which is further rearranged, reduced, or esterified into the other products. These compounds are the first that can be detected upon damage of a plant. There is evidence that "green leaf" volatiles are also inducible (Boland et al. 1995), particularly (Z)-3-hexen-1-yl acetate, which is systemically released by herbivore-damaged cotton (Röse et al. 1996) and could still be detected from maize plants hours after treatment (Fig. 2).

A second group of volatiles comprises monoterpenes and sesquiterpenes of the isoprenoid pathway (Gershenzon and Croteau 1989, 1991; Goodwin and Mercer 1990; Alonso and Croteau 1993). Mevalonic acid was considered to be formed from three acetyl-CoA molecules and subsequently transformed into isopentenyl pyrophosphate from which the building blocks for terpenes are derived. However, Eisenreich et al. (1996, 1997) have demonstrated for several plant terpenoids that they are not of mevalonoid origin. The biosynthesis involved in the induction of some terpenoids has been investigated by Boland and co-workers who found that the homoterpenes (3*E*)-4,8-dimethyl-1,3,7-nonatriene and (3*E*, 7*E*)-4,8,12-trimethyl-1,3,7,11-tridecatetraene are produced from the terpene alcohols nerolidol and geranyllinalool, respectively, through oxidative bond

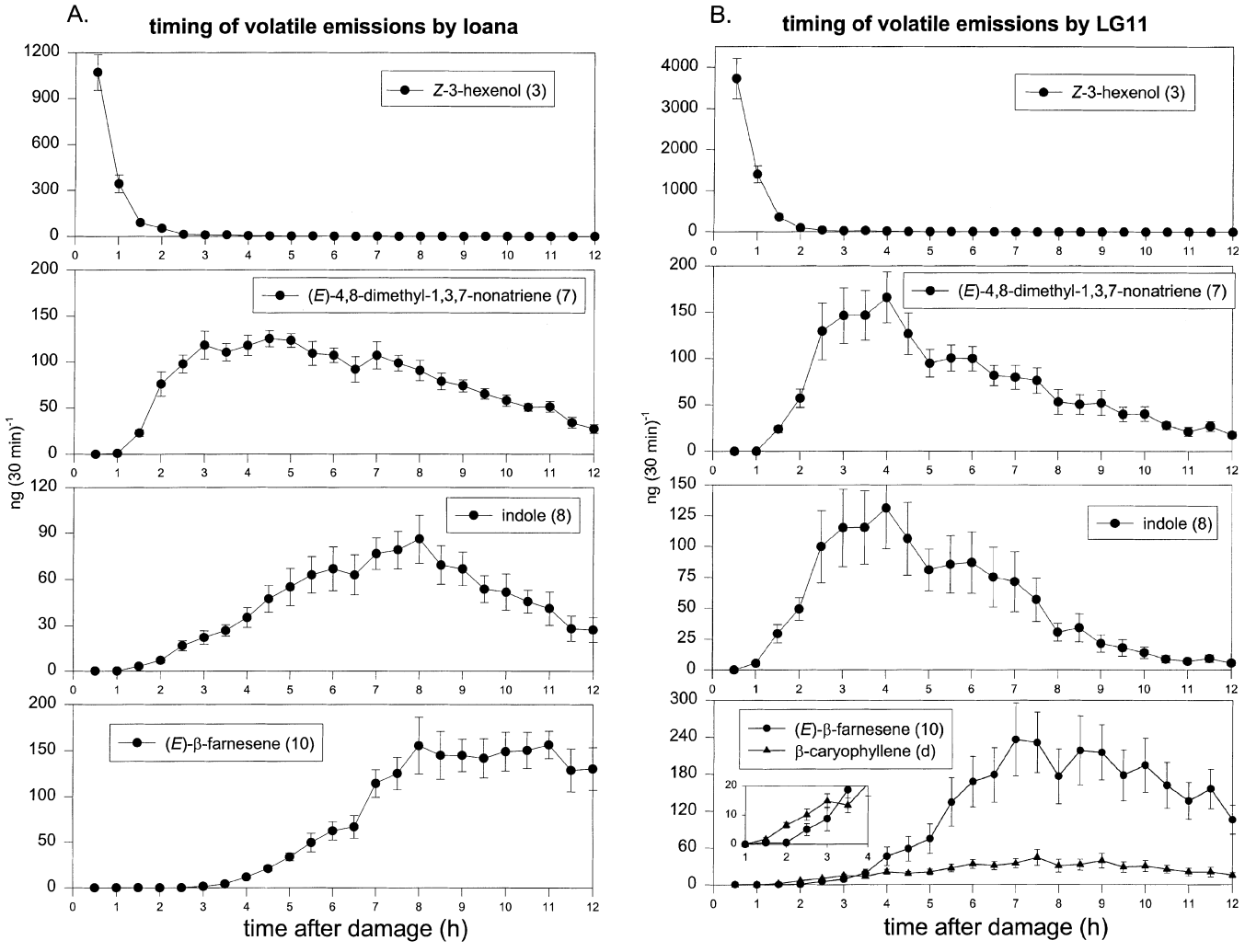

Fig. 3. Emissions of representative compounds from the maize cultivars Ioana (**A**) and LG11 (**B**) over the entire collection period. The number or letter after each compound name corresponds to its peak label in Fig. 2

cleavage (Boland and Gäbler 1989; Gäbler and Boland 1991; Boland et al. 1992). In our study, not all terpenoids were released at the same time and the two cultivars showed considerable differences in the terpenoids emitted. This indicates that the terpenoids are products of more than one biosynthetic route or of different steps within one pathway. The terpenoids linalool, (3*E*)-4,8-dimethyl-1,3,7-nonatriene, (*E*)-α-bergamotene, (*E*)-β-farnesene, and (3*E*,7*E*)-4,8,12-trimethyl-1,3,7,11-tridecatetraene are released by a range (at least 12) of maize genotypes that we have looked at over the years (data not shown). Nerolidol is also released by all genotypes, but in some cases only in trace amounts. In contrast, the terpenoids β-myrcene, (Z)-β-ocimene, β-caryophyllene, and (*E*,*E*)-α-farnesene are released by several, but not all genotypes. Ioana and LG11 represent in this respect two extremes of the spectrum, Ioana releasing very few and LG11 releasing many different compounds.

The two cultivars also differ considerably in the release of volatiles that result from the shikimic acid pathway. This third pathway results in the production of indole, methyl salicylate, and probably the two remaining compounds that we collected, benzyl acetate and phenethyl acetate (Paré and Tumlinson 1996, 1997b). Of these, Ioana only released indole, while LG11 released all four compounds. Ioana and LG11 also differed in the timing of indole release; peak production was considerably earlier for LG11.

Cotton is another plant which has been investigated for its releases of volatiles in response to caterpillar damage (McCall et al. 1993; Loughrin et al. 1994; Röse et al. 1996). In cotton it takes at least a day before induced volatiles can be detected (Loughrin et al. 1994; Röse et al. 1996). These induced terpenoids and indole in response to herbivory are the result of a de-novo synthesis (Paré and Tumlinson 1997a,b). Like many other perennials, however, cotton also possesses constitutive defence chemicals that are stored in specialised glands (Elzen et al. 1985). Among the stored substances are α- and β-pinene, α-caryophyllene, and α-humulene (Loughrin et al. 1994). Unlike the induced terpenoids, these compounds are not synthesised de-novo in

response to herbivory (Paré and Tumlinson 1997a,b), and their emission is instantaneous upon plant damage and ceases rapidly when an attack stops (Loughrin et al. 1994).

Our results indicate that the plant reaction occurs in steps. The first volatiles released immediately after damage are the "green leafy" odours. Parasitoids and predators of herbivores could use these volatiles as cues to pinpoint the location where the herbivores were last feeding. Some hours later the induced compounds are released and they continue to be emitted long after initial damage. These induced compounds are released in large amounts systemically throughout the plant (Turlings and Tumlinson 1992), and may be used by natural enemies of herbivores to locate plants that carry potential prey. The difference in blends emitted by the genotypes Ioana and LG11 reveals a different dimension to the complexity and variety of plant find volatiles and other signals that natural enemies have to select from to find suitable prey and hosts. Some of the compounds [i.e. linalool and (3*E*)-4,8-dimethyl-1,3,7-nonatriene] that are commonly released by most herbivore-damaged plants might be more attractive to generalists than the less common compounds. However, parasitic wasps appear able to learn to use any odour that reliably guides them to hosts in a particular environment (Lewis and Tumlinson 1988; Turlings et al. 1993b; Vet et al. 1995). It is therefore likely that the entire blend of odours released by a specific plant can be used as a signal.

The recent elucidation of the elicitor volicitin from caterpillar regurgitant (Alborn et al. 1997) provides new insight into the mechanisms that are involved in herbivore-induced plant odours and allows us to test ecological hypotheses. Whether or not the reaction in the plant has evolved for the purpose of attracting natural enemies of herbivores remains uncertain (Faeth 1994; Turlings and Benrey 1998). It is clear, however, that the plant odours are essential for prey and host location by predators and parasitoids. The rapid response that we observed in maize will enable the natural enemies of caterpillars to locate their victims at a very early stage of herbivory.

We are grateful to Ara Manukian (Analytical Research Systems, Gainesville, Fla., USA) for advice on the design and use of the volatile-collection apparatus. Jim Tumlinson and Paul Paré (USDA-ARS, Gainesville, Fla., USA), Sandrine Gouinguené, Nicole Kalberer and Thomas Degen (University of Neuchâtel, Switzerland) and two anonymous reviewers provided useful comments on an earlier version of this paper. We thank Claude Fornallaz for technical support, and Prof. Silvia Dorn and the ETH-Zurich for providing us with an excellent infrastructure.

References

Agelopoulos NA, Keller MA (1994) Plant-natural enemy association in the tritrophic system *Cotesia rubecula-Pieris rapae-Brassicaceae* (Cruciferae). I: Sources of infochemicals. J Chem Ecol 20: 1725–1734

Alborn HT, Turlings TCJ, Jones TH, Stenhagen G, Loughrin JH, Tumlinson JH (1997) An elicitor of plant volatiles from beet armyworm oral secretion. Science 276: 945–949

Alonso WR, Croteau R (1993) Prenyltransferases and cyclases. Methods Plant Biochem 9: 239–260

Baldwin IT (1994) Chemical changes rapidly induced by folivory. In: Bernays EA (ed) Insect-plant interactions vol. V. CRC Press, Boca Raton, pp 1–23

Boland W, Gäbler A (1989) Biosynthesis of homoterpenses in higher plants. Helv Chem Acta 72: 247–253

Boland W, Feng Z, Donath J, Gäbler A (1992) Are acyclic C_{11} and C_{16} homoterpenes plant volatiles indicating herbivory? Naturwissenschaften 79: 368–371

Boland W, Hopke J, Donath J, Nüske J, Bublitz F (1995) Jasmonsäure- und Coronatin-induzierte Duftproduktion in Pflanzen. Angew Chem 107: 1715–1717

Dicke M, Sabelis MW (1988) How plants obtain predatory mites as bodyguards. Neth J Zool 38: 148–165

Dicke M, Sabelis MW, Takabayashi J, Bruin J, Posthumus MA (1990) Plant strategies of manipulating predator-prey interactions through allelochemicals: prospects for application in pest control. J Chem Ecol 16: 3091–3118

Edwards PJ, Wratten SD (1985) Induced plant defences against insect grazing: fact or artefact? Oikos 44: 70–74

Eisenreich W, Menhard B, Hylands PJ, Zenk MH (1996) Studies on the biosynthesis of taxol: the taxane carbon skeleton is not of mevalonoid origin. Proc Natl Acad Sci USA 93: 6431–6436

Eisenreich W, Sagner S, Zenk MH, Bacher A (1997) Monoterpenoid essential oils are not of mevalonoid origin. Tetrahedron Lett 38: 3889–3892

Elzen GW, Williams HJ, Bell AA, Stipanovic RD, Vinson SB (1985) Quantification of volatile terpenes of glanded and glandless *Gossypium hirsutum* L. cultivars and lines by gas chromatography. J Agric Food Chem 33: 1079–1082

Faeth SH (1992) Interspecific and intraspecific interactions via plant responses to folivery: an experimental test. Ecology 73: 1802–13

Faeth SH (1994) Induced plant responses: effects on parasitoids and other natural enemies of phytophagous insects. In: Hawkins BA, Sheehan W (eds) Parasitoid community ecology. Oxford University Press, pp 245–260

Gäbler A, Boland W (1991) Stereochemical studies on homoterpene biosynthesis in higher plants; mechanistic, phylogenetic, and ecological aspects. Helv Chim Acta 74: 1773–1789

Gershenzon J, Croteau R (1989) Regulation of monoterpene biosynthesis in higher plants. In: Towers GHN, Stafford HA (eds) Biochemistry of the mevalonic acid pathway to terpenoids. Plenum, New York, pp 99–160

Gershenzon J, Croteau R (1991) Terpenoids. In: Rosenthal GA, Berenbaum MR (eds) Herbivores: their interactions with secondary plant metabolites. Academic Press, San Diego, pp 165–219

Goodwin TW, Mercer EI (1990) Introduction to plant biochemistry. Second edn. Pergamon Press, Oxford

Heath RR, Manukian A (1992) Development and evaluation of systems to collect volatile semiochemicals from insects and plants using a charcoal-infused medium for air purification. J Chem Ecol 18: 1209–1226

Heath B, Manukian A (1994) An automated system for use in collecting volatile chemicals released from plants. J Chem Ecol 20: 593–608

Karban R (1992a) Induced resistance and plant density of a native shrub, *Gossypium thurberi*, affects its herbivores. Ecology 74: 1–8

Karban R (1992a) Cost and benefits of induced resistance and plant density of a native shrub, *Gossypium thurberi*. Ecology 74: 9–19

Lewis WJ, Tumlinson JH (1988) Host detection by chemically mediated associative learning in a parasitic wasp. Nature 331: 257–259

Loughrin JH, Manukian A, Heath RR, Turlings TCJ, Tumlinson JH (1994) Diurnal cycle of emission of induced volatile terpenoids by herbivore-injured cotton. Proc Natl Acad Sci USA 91: 11836–11840

Mattiacci L, Dicke M, Posthumus MA (1995) Beta-glucosidase: an elicitor of herbivore-induced plant odor that attracts host searching parasitic wasps. Proc Natl Acad Sci USA 92: 2036–2040

McCall PJ, Turlings TCJ, Lewis WJ, Tumlinson JH (1993) Role of plant volatiles in host location by the specialist parasitoid

Microplitis croceipes Cresson (Braconidae: Hymenoptera). J Insect Behav 6: 625–639

McCall PJ, Turlings TCJ, Loughrin J, Proveaux AT, Tumlinson JH (1994) Herbivore-induced volatile emissions from cotton (*Gossypium hirsutum* L.) seedlings. J Chem Ecol 20: 3039–3050

Paré PW, Tumlinson JH (1996) Volatile signals in response to herbivore feeding. Fla Entomol 79: 93–103

Paré PW, Tumlinson JH (1997a) Induced synthesis of plant volatiles. Nature 385: 30–31

Paré PW, Tumlinson JH (1997b) De novo biosynthesis of volatiles induced by insect herbivory in cotton plants. Plant Physiol 114: 1161–1167

Rhoades DF (1979) Evolution of plant chemical defense against herbivores. In: Rosenthal GA, Janzen DJ (eds) Herbivores: their interactions with secondary plant metabolites. Academic Press, New York, pp 3–54

Röse USR, Manukian A, Heath RR, Tumlinson JH (1996) Volatile semiochemicals released from undamaged cotton leaves. Plant Physiol 111: 487–495

Schultz JC (1998) Plant responses induced by herbivores. Tree 3: 45–49

Steinberg S, Dicke M, Vet LEM (1993) Relative importance of infochemicals from first and second trophic level in long-range host location by the larval parasitoid *Cotesia glomerata*. J Chem Ecol 19: 47–60

Tallamy DW, Raupp MJ (1991) Phytochemical induction by herbivores. Wiley, New York

Turlings TCJ, Tumlinson JH (1992) Systemic chemical signalling by herbivore-injured corn. Proc Natl Acad Sci USA 89: 8399–8402

Turlings TCJ, Benrey B (1998) Effects of plant metabolites on the behavior and development of parasitic wasps. Écoscience 5: 321–333

Turlings TCJ, Tumlinson JH, Lewis WJ (1990) Exploitation of herbivore-induced plant odors by host-seeking parasitic wasps. Science 250: 1251–1253

Turlings TCJ, Alborn HT, McCall PJ, Tumlinson JH (1993a) An elicitor in caterpillar oral secretions that induces corn seedlings to emit volatiles attractive to parasitic wasps. J Chem Ecol 19: 411–425

Turlings TCJ, Wäckers F, Vet LEM, Lewis WJ, Tumlinson JH (1993b) Learning of host-finding cues by hymenopterous parasitoids. In: Papaj DR, Lewis A (eds) Insect learning: ecological and evolutionary perspectives. Chapman & Hall, New York, pp 51–78

Turlings TCJ, Loughrin JH, Röse U, McCall PJ, Lewis WJ, Tumlinson JH (1995) How caterpillar-damaged plants protect themselves by attracting parasitic wasps. Proc Natl Acad Sci USA 9: 4169–4174

Turlings TCJ, Bernasconi ML, Bertossa R, Bigler F, Caloz G, Dorn S (1998) The induction of volatile emissions in maize by three herbivore species with different feeding habits: possible consequences for their natural enemies. Biol Control 11: 122–129

Vet LEM, Lewis WJ, Cardé RT (1995) Parasitoid foraging and learning. In: Cardé RT, Bell WJ (eds) Chemical ecology of insects. vol 2. Chapman & Hall, New York, pp 65–101