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Biochemical Systematics and Ecology 35 (2007) 68–74
biochemical systematics and ecology
www.elsevier.com/locate/biochemsyseco

Changes in composition of essential oils and volatile emissions of *Minthostachys mollis*, induced by leaf punctures of *Liriomyza huidobrensis*

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Received 2 May 2006; accepted 24 August 2006

Abstract

Plant defensive mechanisms against herbivores include chemical changes following damage. Effects of feeding punctures produced by *Liriomyza huidobrensis* (pea leafminers) adult females on the plant's dominant monoterpenes, pulegone and menthone were assessed by monitoring essential oil composition at 24, 48, and 120 h; emission of volatiles was also measured 24 and 48 h after wounding. We studied such changes in *Minthostachys mollis*, a Lamiaceae species native to Central Argentina with medicinal and aromatic uses. Leaf puncturing resulted in reduced menthone throughout the experiment and increased pulegone concentration in *M. mollis* essential oil during the first 48 h. The adjacent undamaged leaves showed similar changes, suggesting a systemic response. Composition of volatiles released from damaged leaves was also altered, most noticeably by increasing pulegone and diminishing menthone emissions. Such herbivore-induced chemical changes in aromatic plants are economically relevant, since the quality of essential oils and volatile emissions are altered.

Keywords: Phytochemical induction; Aromatic plants; Monoterpenes; Pulegone; Menthone; *Minthostachys mollis*; *Liriomyza huidobrensis*

1. Introduction

Chemical changes induced by mechanical damage or insect herbivore feeding have been observed widely in plants (Karban and Baldwin, 1997; Kessler and Baldwin, 2001). Such changes occur at the site of injury or systemically, and persist for periods ranging from days (Paré and Tumlinson, 1999) to years (Clausen et al., 1991). Many biochemical mechanisms used by plants are direct defenses, whereby herbivores or pathogens are repelled (De Moraes et al., 2001;

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0305-1978/$ - see front matter © 2006 Elsevier Ltd. All rights reserved.
doi:10.1016/j.bse.2006.08.007

Kessler and Baldwin, 2001) or poisoned (Vancanneyt et al., 2001; Andersen et al., 1994). Herbivore-induced volatile compounds may act as indirect defenses, attracting arthropods that prey upon or parasitize the herbivores (Baldwin and Preston, 1999; Thaler, 1999), and thus minimizing further damage to plant tissues (Paré and Tumlinson, 1999; Dicke and Van Loon, 2000). The same chemical response may simultaneously involve both types of defense activity, e.g. compounds that slow herbivore growth by reducing digestive efficiency, may not function as defenses without the third trophic level (the parasitoid), because slow-growing herbivores may eat more leaf material to complete development than fast-growing herbivores, causing a greater level of damage to the plant (De Leo et al., 1998).

Many secondary plant metabolites with presumed defensive roles have herbivore-inducible biosynthetic pathways (Baldwin and Preston, 1999), and their induction has been interpreted as optimizing defense (Stout et al., 1996). Among them, monoterpenoids, the major constituents of plant essential oils are typically volatile and lipophilic properties, which enable them to penetrate rapidly into insects and interfere with their physiological functions (Croteau et al., 2000; Ennan, 2001; Lee et al., 2003). Monoterpenoids are effective as repellents, feeding suppressors, and insecticides against a variety of insects and pathogens (Langenheim, 1994; Isman, 2000; Ciccia et al., 2000; Bekele and Hassanali, 2001; Harrewijn et al., 2001; Ennan, 2001).

Induced chemical changes in aromatic or medicinal plants, particularly those affecting specific compounds with aromatic or therapeutic attributes, have economic importance. Yields of essential oil bearing plants are strongly influenced by environmental factors (Sangwan et al., 2001), although effects of mechanical damage and insect herbivory on composition and production of essential oils have only recently begun to be assessed (Valladares et al., 2002). Changes in essential oils or released volatiles have been observed following mechanical damage (Zabaras and Wyllie, 2001; Zabaras et al., 2002; Banchio et al., 2005a). Induced chemical changes in aromatic plants vary depending on the type of damage (Banchio et al., 2005b), although only within-plant essential oil composition has been evaluated in this regard.

The specific research question reach in the present study was: what kind of chemical changes occur in the composition of essential oils of *Minthostachys mollis* (Kunth.), after the feeding punctures made by *Liriomyza huidobrensis* (Blanchard) (Diptera: Agromyzidae). *M. mollis* (Lamiaceae) is native to Central Argentina with medicinal and aromatic uses in the region.

2. Materials and methods

2.1. Bioassays

M. mollis (Kunth.) Griseb, a perennial shrub 0.30–2.0 m high, grows in the mountainous areas of Córdoba at altitudes between 700 and 1200 m. It is among the most intensively harvested aromatic species in Argentina. Due to its menthol content its aroma resembles that of mint. It is valued for its digestive effects and is also used in industry.

Healthy, pest-free, 6-month-old *M. mollis* plants (average 18 leaves) grown in a glasshouse without supplementary lighting were used. Plants were exposed to adult female *L. huidobrensis*, which had been reared from larvae collected from *Vicia faba* crops in Córdoba city, Central Argentina. *L. huidobrensis* are small (2–3 mm), shiny black and yellow flies that attack a wide range of vegetable and ornamental crops, laying their eggs inside leaves such that the larvae feed between the leaf surfaces (''leaf mining''). Adult female agromyzids characteristically feed by puncturing leaf tissues with their ovipositor and then sucking up exuded cellular contents. When punctures are numerous, reduced photosynthesis, leaf stippling, and early abscission may result (Parella, 1987).

Plants were placed in an entomological cage and exposed to ~30 insects for 4–6 h. Conditions of light, temperature (22 ± 2 °C), and relative humidity (~70%) were similar for all experiments. On each plant, at least five leaves (of similar age and size) from different nodes were exposed to the insects. A ''damage-adjacent'' leaf opposite each experimental leaf was covered with a thin plastic film to prevent feeding by insects. Overall physical damage to the plant was not allowed to exceed 40% of total leaf area, similar to levels observed in nature. After the 4–6 h of insect exposure, plants were transferred to an insect-free environment, and the plastic films were removed from the damage-adjacent leaves. After 24, 48, or 120 h damaged leaves and damage-adjacent leaves were excised, and assessed for chemical induction and translocation effects. Film-covered and -uncovered leaves ($n = 5$) from a non-insect-exposed plant similar in size and age to the experimental plant were used as controls for the damage-adjacent leaves and damaged leaves, respectively. Different plants were used for each treatment. An individual plant was the unit of replication. The youngest and oldest pairs of leaves

were excluded from the analyses. All leaves were kept frozen until chemical analysis, not affecting the stability of specific compounds. Five to ten different plants (units of replications) were used for each experimental treatment.

2.2. Extraction of essential oils, and collection of plant volatiles

Each plant sample was weighed and subjected to hydrodistillation in a micro-Clevenger-like apparatus for 40 min, and the volatile fraction was collected in dichloromethane. Internal standard was added (12 μg thymol in 2 ml dichloromethane). Essential oils of *M. mollis* comprise 50 different compounds, with two monoterpenes accounting for about 70% of total volume: pulegone = cyclohexanone, 5-methyl-2-(1-methylethylidene); and menthone = cyclohexanone, 5-methyl-2(1-methylethyl) (Valladares et al., 2002). These two compounds were quantified with respect to thymol, which was added during the distillation procedure. Flame Ionization Detector (FID) response factors for each compound generated equivalent areas with negligible difference (<5%).

Essential oil composition of control film-covered leaves did not differ significantly from that of uncovered leaves on the same plant (Wilcoxon signed-ranks test, $P > 0.05$), thus ruling out possible effects of the film cover.

The volatile collection system consisted of a vacuum pump that created a constant airflow (300 ml/min) through a polyethylene terephthalate (PET) chamber (1500 ml volume) containing a plant (damaged or undamaged). The chamber was closed at one end with a cap pre-drilled to exactly fit the collection trap. At the other end a cap, with a hole through which the plant stem passed, separated the bottom of the chamber from the plant pot ground. Air exited the chamber throughout a reusable glass collection trap packet with 30 mg Super-Q absorbent (80–100 mesh; Alltech), which was rinsed with 5–10 ml dichloromethane prior to each volatile collection to remove impurities. Volatile compounds were collected for 2 h, then immediately eluted from the absorbent traps with 200 μl dichloromethane, and internal standard was added (12 μg thymol in 2 μl dichloromethane). Collected volatiles were analysed by gas chromatography as described below. Following collection of volatiles, the plant was cut and weighed.

For experimental plants, volatiles were collected 24 and 48 h after damage. Volatiles were also collected from control (undamaged) plants. Collections from an empty chamber showed that background level of monoterpenes was negligible.

2.3. Chemical analysis

Chemical analyses were performed using a Perkin–Elmer Q-700 gas chromatograph equipped with a CBP-1 capillary column (30 m × 0.25 mm, film thickness 0.25 μm) and a mass-selective detector. Analytical conditions: injector and detector temperatures 250 and 270 °C, respectively; oven temperature programmed from 60 °C (3 min) to 240 °C at 4 °C/min; carrier gas = helium at a constant flow of 0.9 ml/min; source 70 eV. Oil components were identified based on mass spectral and retention time data, which were compared with those of standard compounds and with those published in Zygadlo et al. (1996). GC analyses were performed using a Shimadzu GC-RIA gas chromatograph, fitted with a 30 m × 0.25 mm fused silica capillary column coated with Supelcowax 10 (film thickness 0.25 μm). GC operating conditions: oven temperature programmed from 60 °C (3 min) to 240 °C at 4 °C/min, injector and detector temperatures 250 °C; detector FID; carrier gas = nitrogen at a constant flow of 0.9 ml/min.

2.4. Volatile emission rate

The amount of monoterpenes emitted relative to their content in plant tissues was estimated as concentration of menthone (or pulegone) in the headspace divided by concentration in the essential oil (headspace/essential oil).

2.5. Statistical analyses

Differences in menthone and pulegone content among treatments from independent samples were analysed by Kruskall–Wallis test, since data were not normally distributed. Comparisons between damaged vs. damage-adjacent leaves were made by Wilcoxon signed rank test (paired samples). Data analyses were performed using INFOSTAT 2.0 software.

3. Results

3.1. Oil concentration

The concentration of menthone (Fig. 1a) in the essential oil of punctured leaves decreased significantly after 24 h and remained lower than in control leaves at 48 and 120 h ($P = 0.04$, Kruskall–Wallis $H = 8.51$). Pulegone (Fig. 1b) showed a twofold increase ($P = 0.001$, Kruskall–Wallis $H = 15.12$) in punctured leaves during the first 48 h, and then decreased to pre-damage levels.

The chemical changes observed in leaves punctured by the insect were translocated to adjacent leaves (Fig. 1a, b), since both menthone and pulegone levels in damage-adjacent leaves were similar to those in damaged leaves ($P_{\text{menthone 24 h}} = 0.10$, $P_{\text{menthone 48 h}} = 0.40$, $P_{\text{menthone 120 h}} = 0.19$, $P_{\text{pulegone 24 h}} = 0.34$, $P_{\text{pulegone 48 h}} = 0.64$, $P_{\text{pulegone 120 h}} = 0.34$, Wilcoxon signed rank test).

3.2. Plant volatiles

In headspace experiments, concentrations of compounds emitted by damaged vs. undamaged plants were different. Emission of menthone from damaged plants was similar to that from undamaged plants when measured 24 h after insect exposure ($P = 0.02$, Kruskall–Wallis $H = 7.95$), but decreased to 90% of baseline level after 48 h (Table 1). In contrast, emission of pulegone increased up to 8.4-fold in damaged plants ($P = 0.01$, Kruskall–Wallis $H = 13.04$), with highest levels observed after 24 h (Table 1).

3.3. Emission rate of volatiles

The emission rate of pulegone relative to its concentration in the essential oil did not show significant changes following damage. In contrast, the emission rate of menthone after 48 h was dramatically lower in damaged compared to undamaged plants (Fig. 2).

4. Discussion

Leaf punctures by adult female *L. huidobrensis* induced a decrease in menthone and increase in pulegone content in the essential oil of *M. mollis*. This plant response is consistent with those observed previously for leaf punctures and other insect feeding habits (chewing and sap sucking), but differs from responses to mechanical damage and feeding by thrips (Banchio et al., 2005a,b). The decreased menthone levels were maintained for at least 120 h after leaf puncture (at which time initiation of mining was not yet visible), whereas pulegone greatly increased 48 h after damage but returned to baseline level by 120 h. These results suggest changes in the biosynthetic processes of *M. mollis* during a 1–5-day period following feeding by leafminer females. Such rapid chemical changes may be interpreted as an attempt to minimize subsequent predation (Clausen et al., 1991).

Monoterpenes are induced by herbivore feeding in *M. mollis* (Valladares et al., 2002; Banchio et al., 2005b) and in other plants species (e.g. McAuslane et al., 1997; Paré and Tumlinson, 1999). Their apparent role in protecting

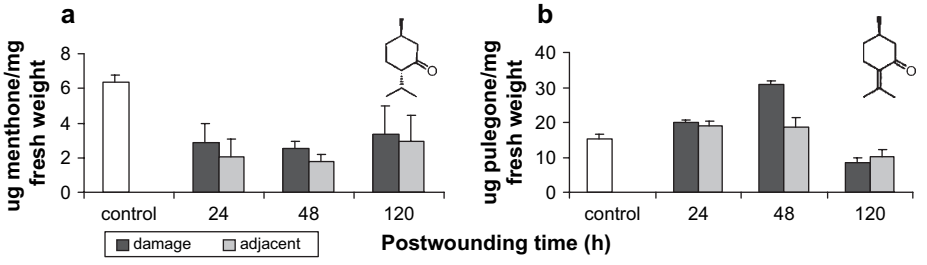

Fig. 1. Changes in oil concentration (mean ± SE) of (a) menthone and (b) pulegone from *M. mollis* leaves as a result of leaf puncture by adult female *L. huidobrensis*.

Table 1
Variation in the main volatiles released from *Minthostachys mollis* plants as a result of feeding punctures by adult female *Liriomyza huidobrensis*

Compound	Control	24 h post-wounding	48 h post-wounding
Menthone	1.13 ± 0.14	1.59 ± 0.03	0.12 ± 0.05
Pulegone	0.21 ± 0.03	1.78 ± 0.21	1.35 ± 0.31

Values are expressed in ng/mg fresh weight (mean ± SE). Significant differences were detected by Kruskall–Wallis test (see text).

damaged leaves from further attack can be attributed mainly to pulegone, a potent inhibitor of acetylcholinesterase (AchE) in invertebrates. AchE is a neurotransmitter that regulates the function of brain as well as heart, lungs, and skeletal muscles. Inhibition of AchE kills insects by blocking the enzyme until their nervous systems do not function properly (Harrewijn et al., 2001; Rice and Coats, 1994; Lee et al., 2003). Pulegone has been shown to cause repellent effect (Mason, 1990), toxicity (Fournet et al., 1996; Franzios et al., 1997; Ellis and Baxendale, 1997; Lamiri et al., 2001; Harrewijn et al., 2001), and interference with development and reproduction (Hummelbrunner and Isman, 2001) in various insect species. It can also create a biochemical barrier to host plant utilisation, by destroying herbivore symbionts (Harrewijn et al., 2001). Menthone shows a weaker insecticidal (Lee et al., 2001) and genotoxic activity (Franzios et al., 1997); however, its decrease after leaf damage may enhance the toxic effect of pulegone, since the two compounds seem to be antagonistic (Franzios et al., 1997).

The present results indicate a translocation of the plant response, since menthone and pulegone levels were not significantly different in damaged vs. damage-adjacent leaves. Systemic responses have been reported in other plant systems, and attributed to signalling molecules, which allow communication among different plant tissues (McAuslane et al., 1997; Constabel and Ryan, 1998; Baldwin and Preston, 1999; Harbone, 2001; Gatehouse, 2002). Elicitors, associated in some cases with insect saliva, may be involved in systemic plant responses (Turlings et al., 2000). Saliva cannot be the elicitor in the present case, because the female leafminer uses its ovipositor to puncture leaf epidermal cells. Other possible factors triggering systemic plant responses include number of wounded cells in contact with healthy cells (Lin et al., 1990), cell or tissue types affected by damage, and types of forces acting on the leaf (Baldwin and Preston, 1999; Dicke and Hilker, 2003).

Effects of wounding on leaf oil concentration, besides their role in plant protection from herbivory (Isman, 2000) have commercial implications in view of the economic importance of monoterpenes for the fragrance, flavour, and pharmaceutical industries. Oil composition of peppermint (*Mentha piperita*), a close relative of *M. mollis*, is adversely affected by conditions that favour the production and accumulation of pulegone, thereby giving an "off" odour and taste (Mahmoud and Croteau, 2002).

Leaf punctures from adult leafminer feeding affected the release of volatile terpenoids in *M. mollis*, consistent with our previous observations on mechanical damage (Banchio et al., 2005a). The emission of volatile pulegone increased while emission of menthone decreased, reflecting the general response pattern observed in the essential oil. In our study of response of the same plant to mechanical damage, emission of menthone remained unaltered (Banchio et al., 2005a); this is the main point of contrast from the present results.

In aromatic herbs, significant amounts of volatile compounds accumulate in the leaf glandular trichomes and the emitted volatiles represent only a small fraction (usually less than 1%) of the total pool produced (Gershenzon et al.,

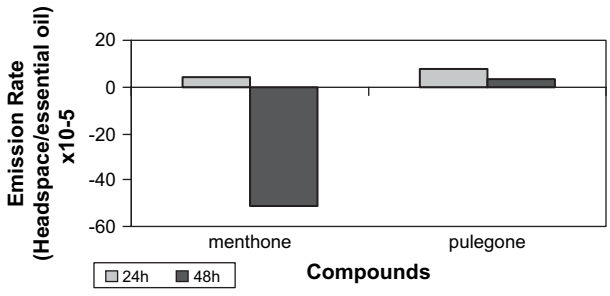

Fig. 2. Volatile emission rates of menthone and pulegone from *M. mollis* plants, 24 and 48 h after leaf puncture by adult female *L. huidobrensis*. Values represent differences from corresponding rates in undamaged plants.

2000; Tyson et al., 1974). Proportions of emitted monoterpenes may differ from those in the plant oil (Werker, 1993; Guillet et al., 1998; Gershenzon et al., 2000). In undamaged *M. mollis* plants, volatile emissions are mainly menthone, whereas the essential oil within the plant contains the pulegone as the major component (Banchio et al., 2005a). Following leaf puncture by female *L. huidobrensis*, the emission rate of volatile menthone showed a great decrease at 48 h. At that point, pulegone became the dominant component of both the essential oil and the emitted volatiles.

Acknowledgements

This research was supported by a grant from Consejo Nacional de Investigaciones Científicas y Tecnológicas.GV, JZ, and WG are Career Member of the Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET) of the República Argentina. EB, PB and LR have a fellowship from the CONICET.

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