

Original Research

# *Apion miniatum* Germ. Herbivory on the Mossy Sorrel, *Rumex confertus* Willd.: Induced Plant Volatiles and Weevil Orientation Responses

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## Abstract

In this paper we report on the large induction of volatile organic compounds (VOCs) from a single leaf of the mossy sorrel, *Rumex confertus* Willd. (Polygonaceae), by herbivory of the red dock weevil (*Apion miniatum* Germ., Coleoptera: Apionidae). VOC blends induced by the red dock weevil herbivory included 5 green leaf volatiles (GLVs) ((Z)-3-hexenal, (E)-2-hexenal, (Z)-3-hexenol, (E)-2-hexenol, (Z)-3-hexen-1-yl acetate), two esters (benzyl acetate, methyl salicylate), and four terpenes ((Z)- $\beta$ -ocimene, linalool,  $\beta$ -caryophyllene, (E)- $\beta$ -farnesene). Not surprisingly, uninjured plants produced only small amounts of VOCs. A Y-tube experiment revealed that females of *A. miniatum* were attracted to the blend (blend 1) of (Z)-3-hexenal + (E)-2-hexenal + (Z)-3-hexenol + (E)-2-hexenol + (Z)-3-hexen-1-yl acetate at two concentrations of 1 and 5 ng·min<sup>-1</sup>. In contrast males of the red dock weevil were not attracted to any tested concentration. Moreover, females and males of *A. miniatum* were not attracted to any concentration of blend 2 ((Z)-ocimene + linalool + benzyl acetate + methyl salicylate +  $\beta$ -caryophyllene + (E)- $\beta$ -farnesene). Yet the red dock weevil females and males were repelled by the highest concentration (125 ng·min<sup>-1</sup>) for both blends.

**Keywords:** *Apion miniatum*, red dock weevil, mossy sorrel, odors

## Introduction

Plants are vulnerable to attack by organisms during their life, but even being immobile are not merely passive victims [1, 2]. To protect themselves they have evolved an arsenal of physical and chemical defences [3-8]. There are many types of VOCs released by plants in response to insect attack (terpenes, fatty acid derivatives, benzenoids,

phenyl propanoids, and amino acid-derived metabolites) [9, 10]. Plant VOCs can be constitutively expressed, while those quantitatively or qualitatively induced after herbivory are often called herbivore-induced plant volatiles (HIPVs) [11, 12]. Plant-induced VOCs defensive functions include directly deterring herbivores [13, 14], indirectly attracting natural enemies of attackers [15] and priming defences of uninjured organs on the same plant [16, 17]. Thus uninjured plants can prime their metabolic machinery without investment costs of actual defence induction [18]. Yet a caveat of

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caution needs to be pointed out concerning ecological and evolutionary aspects of VOC induction [19]. An insect dose response to an individual plants VOCs can reveal the range of concentrations over which herbivore or parasitoid attraction or repellence occurs. A dose response to a VOC should indicate herbivore or predator or parasitoid sensitivity to a compound. By comparing dose responses across different VOCs induced after plant attack, the relative importance of VOCs can be suggested for primary and secondary consumers.

We examined interactions between *Rumex confertus* Willd. (Polygonaceae) and *Apion miniatum* Germ. (Coleoptera: Apionidae). Many *Rumex* spp. are serious weeds. Members of this family are very common perennial herbs growing mainly in the northern hemisphere, but various species have been introduced almost everywhere. In Western Australia, *Rumex pulcher* L. populations were greatly reduced in sites where *Pyropteron dorylififormis* Ochsenheimer (Lepidoptera: Sesiidae) had been released [20]. In northern Victoria *P. dorylififormis* (dock moth) established well on *R. crispus* [21, 22]. Moreover, *Rumex* species are used as food plants by the larvae of a number of *Lepidoptera* species. This is an interesting system involving a possible biological control agent of an invasive weed in Eastern Europe [23]. Classical biological control of weeds via the introduction of natural enemies from the native habitat of the weed is one of the most important methods to manage alien invasive weeds [24, 25] confirmed larval the development of *Apion* sp. in *Miconia calvescens* De Candolle (Melastomataceae) fruits. They found that the presence of *Apion* sp. on *M. calvescens* inflorescences is likely due to oviposition and feeding. Surveys in Israel in 1988 showed that the apionid weevil *A. miniatum* Germ. (Coleoptera: Apionidae) was damaging on *Emex spinosa* (L.) Campd. Subter. The larvae of *A. miniatum* develop in the stems, crown, and roots, and the adults make small holes in leaves of *E. spinosa* (Polygonaceae) [26]. The progression of the various biological control projects gives the opportunity to improve the science behind biological control and particularly to improve the safety, efficiency and efficacy of projects [27].

In the present study, we identified VOCs induced by a single *R. confertus* leaf after *A. miniatum* herbivory. We examined *R. confertus* constitutive and induced VOC emissions after *A. miniatum* herbivory to suggest VOCs of interest to test *A. miniatum* responses. Subsequently, we used Y-tube behavioral experiments to test blend 1 and blend 2 responses of adult males and females of *A. miniatum* to five GLVs and six VOCs induced by *R. confertus* (to examine attraction/avoidance to injured and uninjured leaf *R. confertus* VOCs).

## Experimental Procedures

### Plant Culture

Experiments were performed in 2011 at the University of Technology and Life Sciences, Bydgoszcz, Poland in the

Plant Growth Center (PGC). In April 2010 30 mossy sorrel plants were dug up and transplanted to the PGC. One plant per pot was located in sterilized soil and maintained with supplemental light and ambient humidity. The photoperiod was 16L:8D, daytime temperature was 22±2°C, and overnight temperature was 18±2°C. Two months after transplantation (June 2010), plants were randomly assigned to control and herbivory treatments for the VOC induction experiment.

### Infestation by the Red Dock Weevils

One leaf of each *R. confertus* injury treatment plant was placed into a Nalophan bag (~50 cm high×30 cm diam.; polyethylene terephthalate bags are odor- and taste-free cooking bags made of a plastic film resistant to decomposition in the temperature range from -60°C to +220°C (Charles Frères, Saint Etienne, France). Two newly-emerged pairs recognized by 'in copula' phase (two pairs were used due to lower size in comparison to *Gastroidea* sp.; previous experiments) were introduced to the Nalophane bag with one leaf of a plant while still attached to the plant. The plants were subjected to feeding for 24 h. Weevils began to feed immediately when placed on a leaf placed in the Nalophan bag. The feeding insects were then removed immediately prior to VOC collection. Thus VOCs were measured from the injured leaf and not from the weevils.

### Volatile Collection System (VCS)

Volatiles were collected simultaneously from enclosed *R. confertus* plants from 10 a.m. to 1 p.m. (sunny days during all measurements). Odors were collected for 3h from one leaf (both of each control or injury treatment plant).

Eight days of measurements were required (20 herbivory treatment plants, 10 control plants, and 2 blanks (empty Nalophan bags)), because the VCS apparatus was set up to collect VOCs from four plants simultaneously. A volatile collector trap (6.35-mm-OD (outside diameter), 76-mm-long glass tube; Analytical Research Systems, Inc., Gainesville, Florida, USA) containing 30 mg of Super-Q (Alltech Associates, Inc., Deerfield, Illinois, USA) adsorbent was inserted into each of four Tygon tubes (connection between airflow meter and collector trap). Purified humidified air was delivered at a rate of 60 l·h<sup>-1</sup> over the plants. A vacuum pump sucked 20% less air (48 l·h<sup>-1</sup>) to avoid collecting odors from any gap of the system.

### Analytical Methods

Volatiles were eluted from each Super-Q collection trap with 225 µL of hexane containing 7 ng of decane as an internal standard. Volatiles were analyzed by coupled gas chromatography-mass spectrometry (GC-MS). A GC Perkin Elmer AutoSystem XL was fitted with a 30-m DB-5MS capillary column (0.25-mm-ID, 0.25 µm film thickness; Restek, Bellefonte, PA, USA). The temperature program increased the chromatography oven temperature from

Table 1. Descriptive statistics for values of the VOCs.

VOCs		Min.	Mean	Median	Max.	Sd	Skewness	Kurtosis	CV
Z-3-HAL	treatment	359.8	473.5	491.6	608.7	66.28	-0.0536	-0.6156	14.00
	control	0.5	2.38	2.6	4.2	1.394	-0.0719	-1.491	58.57
E-2-HAL	treatment	34.7	49.85	48.65	64.7	9.479	-0.0552	-1.114	19.02
	control	0.8	1.51	1.4	2.4	0.599	0.435	-1.157	39.67
Z-3-HOL	treatment	34.8	48.88	49.35	61.4	7.144	-0.3233	-0.5303	14.62
	control	0	0.73	0.8	1.4	0.4945	-0.3054	-1.202	67.74
E-2-HOL	treatment	10.1	18.73	19.9	34.2	5.647	0.6156	1.028	30.15
	control	0	0.21	0.2	0.4	0.1595	0.00346	-1.444	75.95
Z-3-HAC	treatment	348.7	504	478.5	658.9	90.38	0.2893	-0.9486	17.93
	control	0.9	3.89	4.4	6.2	1.795	-0.5102	-1.069	46.14
Z-OCI	treatment	86.9	126.6	123.8	178.4	27.38	0.2139	-1.122	21.63
	control	0.4	1.53	1.55	2.4	0.6584	-0.473	-0.8818	43.03
LIN	treatment	345.8	430.1	426.8	604.2	63.15	0.9143	0.9974	14.68
	control	0.4	2.58	2.8	4.7	1.437	-0.1555	-1.202	55.70
BAC	treatment	16.8	26.01	24.7	38.5	6.83	0.3649	-1.019	26.26
	control	0	0.365	0.25	1.2	0.3986	1.009	-0.1056	109.21
MAT	treatment	12.8	25.8	35.15	40.2	8.403	0.08318	-1.197	32.57
	control	0	0.7	0.55	2.1	0.6307	1.02	0.4548	90.10
$\beta$ -CAR	treatment	324.8	392	398.6	462.1	35.74	0.1078	-0.5295	9.12
	control	0.4	1.46	1.45	2.4	0.7486	-0.2658	-1.398	51.27
$\beta$ -FAR	treatment	698.7	837.1	844.2	962.4	64.22	-0.2165	-0.2628	7.67
	control	0.5	2.02	2.25	3.5	1.15	-0.1215	-1.421	56.93

Sd – standard deviation

CV – coefficient of variation [in %]

40°C to 200°C at 5°C·min<sup>-1</sup>. The compounds were ordered on the chromatogram by their retention time and IDs were initially determined by matches to known compounds in the NIST 1998 database. A commercially available standard of each compound was run to confirm each plant VOC ID. Peaks were integrated from each GC-chromatogram and compared to the corresponding internal standard peak to calculate constitutive and induced VOC concentrations.

#### Y-tube *Apion miniatum* Behavior

Weevils were tested with one blend of five synthetic GLVs [(Z)-3-hexenal + (E)-2-hexenal + (Z)-3-hexenol + (E)-2-hexenol + (Z)-3-hexen-1-yl acetate], and a second blend consisting of six VOCs [(Z)-ocimene + linalool + benzyl acetate + methyl salicylate +  $\beta$ -caryophyllene + (E)- $\beta$ -farnesene]. All components (95% purity) were purchased from Sigma-Aldrich. The Y-tube system used was similar to that described by Piesik et al. [28]. Each blend was tested at 5 concentrations (0, 1, 5, 25, 125 ng·min<sup>-1</sup>). Each individual VOC was present in a blend at the specified concen-

tration. Thus for instance for the GLVs blend 1 ng·min<sup>-1</sup> means that 1 ng (Z)-3-hexenal + 1 ng (E)-2-hexenal + 1 ng (Z)-3-hexenol + 1 ng (E)-2-hexenol + 1 ng (Z)-3-hexen-1-yl acetate was added to 50  $\mu$ l hexane. A dose of a blend was placed in one arm of the Y-tube and tested against 50  $\mu$ l hexane without the blend (0 ng·min<sup>-1</sup>). The tubes were washed and rotated to limit the effects of chemical residues from previous bioassay subjects on the current test subject. Of each sex, 20 newly-emerged ( $\leq$ 1-day-old) adults (with fully developed olfactory sensory systems) were tested at each concentration of each blend, with each insect tested once. All tested adults chose an arm of the Y-tube within 3 min.

#### Data Analysis

The descriptive statistics (mean, median, minimal and maximal values, standard deviation, skewness and kurtosis, and coefficient of variation) were used to report the VOCs quantities and their distribution as well as the variations recorded by the GC-MS from the injured and control

leaves. The relationships between 11 compounds were estimated using Pearson's correlation coefficients, since there were no deviations from the normal distribution. All relationships were presented in the form of a scatterplot and the significant correlations in linear form [29].

Chi-square goodness of fit tests ( $X^2$ -test), with the Yates correction for small samples ( $1 \times 2$ ), were conducted to indicate whether the choice of Y-tube arms was influenced by a preference for odor source (plant bouquet vs. hexane solvent; or synthetic blend vs. hexane solvent) at each exposure concentration  $\times$  sex  $\times$  exposure duration combination. Non-significant tests indicated that the observed beetle counts did not significantly deviate from an expected ratio of 10:10 (hexane solvent only arm:plant bouquet or synthetic blend). Significant tests indicated attraction (more individuals chose Y-tube arm with a plant bouquet or synthetic blend) or repellency (more individuals chose the Y-tube arm with only hexane solvent). All statistical tests were conducted using SAS version 9.2 [30] (significance threshold  $\alpha=0.05$ ).

## Results

### Volatiles after Insect-Caused Foliar Damage

The greatest quantities of volatiles released by mossy sorrel plants after injury by red dock weevil were recorded

for  $\beta$ -FAR, Z-3-HAC, Z-3-HAL, LIN, and  $\beta$ -CAR with the mean values respectively: 837, 504, 473, 430, and 399  $\text{ng}\cdot\text{h}^{-1}$ . Much smaller amounts of volatile compounds related to the following: Z-OCI, E-2-HAL, Z-3-HOL, BAC, MAT, and E-2-HOL with the means from 18.7 to 127  $\text{ng}\cdot\text{h}^{-1}$  (Table 1, Fig. 1). Based on the skewness and kurtosis calculations we conclude that results represent the distribution similar to the normality, not exceeding the threshold values. The greatest variations were recorded in the case of MAT and E-2-HOL ( $C_v > 30\%$ ), while the smallest for  $\beta$ -FAR and  $\beta$ -CAR ( $C_v < 10\%$ ). The control plants released trace amounts of VOCs ranging from 0.21 (E-2-HOL) to 3.89  $\text{ng}\cdot\text{h}^{-1}$  (Z-3-HAC) with a very high variability of their release.

The simultaneous release of certain volatile compounds altered positive correlation nature, as in the case of: BAC and Z-3-HOL ( $r=0.51$ ), BAC and Z-OCI ( $r=0.57$ ),  $\beta$ -CAR and Z-OCI ( $r=0.52$ ), and MAT and BAC ( $r=0.4538$ ). Meanwhile a negative relationship was found in the case of Z-OCI and Z-3-HAL ( $r=-0.45$ ), Z-3-HAC, and E-2-HAL ( $r=-0.58$ ), (Fig. 2). For the vast majority of volatile compounds there were no significant relationships, as shown in Fig. 1.

### Y-tube Behavior of *A. minutum*

We found that weevils chose one arm of the Y-tube usually within 2 min. Chi-square tests revealed that female *A.*

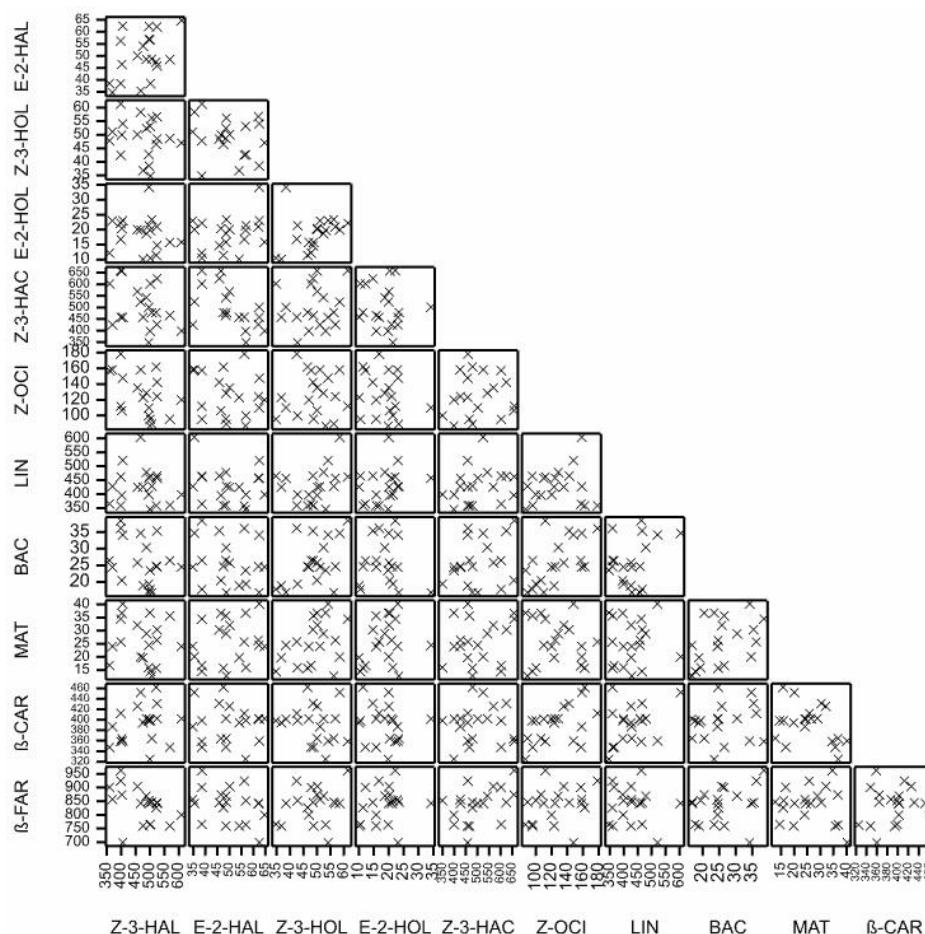


Fig. 1. Scatterplot matrix of relationships among VOCs (Z-3-HAL, E-2-HAL, Z-3-HOL, E-2-HOL, Z-3-HAC, Z-OCI, LIN, BAC, MAT,  $\beta$ -CAR,  $\beta$ -FAR) ( $\text{ng}\cdot\text{h}^{-1}$ ).

Table 2. Effect of one synthetic blend 1 of five GLVs [(Z)-3-HAL + (E)-2-HAL + (Z)-3-HOL + (E)-2-HOL + (Z)-3-HAC], and a second synthetic blend 2 of six VOCs [(Z)-OCI + LIN + BAC + MAT + β-CAR + β-FAR] on the number of *A. miniatum* adult females and males choosing to enter a Y-tube arm containing the blend odor or the Y-tube arm containing purified humidified air and hexane solvent (no odor).

Name of mixed compounds	Dose	ng·min <sup>-1</sup>	+ <sup>(4)</sup>	- <sup>(5)</sup>	χ <sup>2</sup> <sup>(1)</sup>	+ <sup>(4)</sup>	- <sup>(5)</sup>	χ <sup>2</sup> <sup>(1)</sup>
(Z)-3-HAL	control	0.0	10	10	0.05 ns	12	8	0.45 ns
+ (E)-2-HAL	1	1	16	4	6.05* (a) <sup>(3)</sup>	7	13	1.25 ns
+ (Z)-3-HOL	2	5	15	5	4.05* (a) <sup>(3)</sup>	8	12	0.45 ns
+ (E)-2-HOL	3	25	4	16	6.05* (r) <sup>(2)</sup>	11	9	0.05 ns
+ (Z)-3-HAC	4	125	3	17	8.45** (r) <sup>(2)</sup>	5	15	4.05* (r) <sup>(2)</sup>
Z-OCI	control	0.0	12	8	0.45 ns	8	12	0.45 ns
+ LIN	1	1	6	14	2.45 ns	9	11	0.05 ns
+ BAC	2	5	3	17	8.45** (r) <sup>(2)</sup>	7	13	1.25 ns
+ MAT	3	25	3	17	8.45** (r) <sup>(2)</sup>	4	16	6.05* (r) <sup>(2)</sup>
+ β-CAR	4	125	2	18	11.25*** (r) <sup>(2)</sup>	4	16	6.05* (r) <sup>(2)</sup>
+ β-FAR								

<sup>(1)</sup> level of significance (ns-not significant), (\*p<0.05), (\*\*p<0.01), (\*\*p<0.001)

<sup>(2)</sup> r – repellent

<sup>(3)</sup> a – attractant

<sup>(4)</sup> + Y-tube arm with tested amount of the compound, volatile diluted in hexane emitted from filter paper

<sup>(5)</sup> – Y-tube arm only with hexane emitted from filter paper

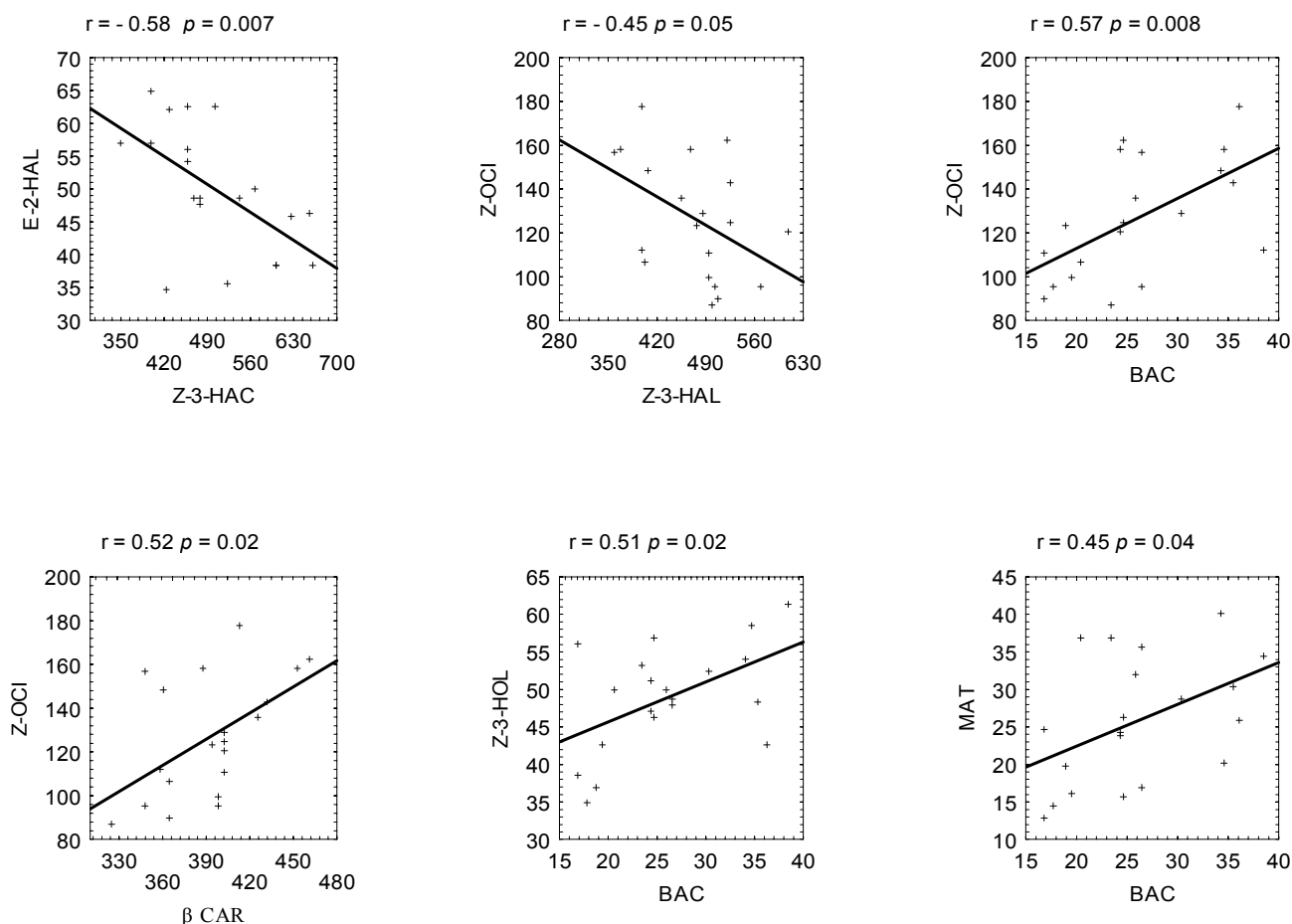


Fig. 2. Significant correlations between amounts of VOC based on r-Pearson coefficients (ng·h<sup>-1</sup>).

*miniatum* were significantly attracted at 1 and 5 ng·min<sup>-1</sup> to blend 1 (Table 2). No attractive concentration for both blends was observed in the responses of males. Yet the red dock weevil females were repelled by the concentrations of 25 and 125 ng·min<sup>-1</sup> for blend 1 and 5, 25, 125 ng·min<sup>-1</sup> for blend 2. Males seemed to be less sensitive and were repelled by one concentration (125 ng·min<sup>-1</sup>) of blend 1 and two concentration (25, 125 ng·min<sup>-1</sup>) of blend 2.

## Discussion of Results

In the first part of our experiment, we confirmed that *A. miniatum* herbivory dramatically induced 11 VOCs from mossy sorrel plants, all of which are common injury-induced GLVs, terpenes, and an aromatic compound [31, 32]. Abiotic injury often induces GLVs while terpene and indole induction often requires actual herbivore feeding injury [33]. However, pathogen infection also can induce GLVs and terpenes [34]. VOCs can be involved in direct and indirect plant defenses against herbivores or pathogens [35, 36]. VOCs were released from control plants only in small but detectable amounts.

In the second Y-tube behavioral experiment, we chose to use equal amounts of each VOC in the blend for a given test dose. Thus the ratios of synthetic blend VOCs encountered by test herbivores likely differ from the ratio of these compounds in natural plant VOC bouquets. Under Y-tube conditions only females of *A. miniatum* responded positively to concentrations 1 and 5 ng·min<sup>-1</sup> of blend 1. However, females were significantly repelled by the highest concentrations of tested blend 1 (25 and 125 ng·min<sup>-1</sup>). Thus females of the red dock weevil might use small amounts of mossy sorrel GLVs for host-plant searching.

The above results are in good agreement with those from the congener *G. viridula* with *R. confertus* [37] and *G. polygoni* with *R. confertus* [38]. Thus herbivory on a single *R. confertus* leaf by *G. polygoni* and *G. viridula* could result in similar adult conspecific and congeneric VOC behavioral responses to injured plants. Our study and both previous studies suggest that *A. miniatum*, *G. polygoni*, and *G. viridula* use GLVs from injured leaves to find lightly injured (single leaf) host plants, but may avoid highly injured plants. This inference depends on the degree of VOC induction increasing with *A. miniatum* herbivory intensity on *R. confertus* and needs to be tested in the field. Piesik et al. [28] found that only female *Cephus cinctus* Norton (Hymenoptera: Cephidae) were attracted to some concentrations of (Z)-3-HAC, (Z)-3-HOL, and the terpene  $\beta$ -ocimene. Yet *C. cinctus* females were repelled by the highest tested concentration (8,400 ng·h<sup>-1</sup>) of (Z)-3-HAC. With maize (VOCs induced by *Fusarium infection*), behavioral tests found attraction to synthetic components for adult cereal leaf beetles *Oulema melanopus* L. (Coleoptera: Chrysomelidae) at 7,500 ng·h<sup>-1</sup> for two GLVs ((Z)-3-HAL, (Z)-3-HAC) and two terpenes (LIN &  $\beta$ -CAR), and attraction at lower doses of 60 ng·h<sup>-1</sup> for both GLVs and 300 ng·h<sup>-1</sup> for LIN. In contrast, Carroll et al. [39]

showed with Y-tube tests that crawling larval *Spodoptera frugiperda* Walker (Lepidoptera: Noctuidae) were attracted to injured maize over uninjured plants, to a wide range of LIN concentrations, and undamaged plants with LIN added (and even linalool alone) were much more attractive than uninjured plant bouquets. There are often synergistic effects of VOC blends on insect attraction or repellence, so only certain VOCs of a plant bouquet may influence insect behavior [40, 41].

VOC induction effects on plants will need further investigation to explore the ecological role of these active substances [42]. It is well known that manipulation of volatile emission in plants has enormous potential in relationship to pest management in agricultural contexts [43]. Manipulating these signals may help increase the effectiveness of attracting parasitoid and predatory natural enemies with induced VOCs to more effectively serve as biological control agents in agroecosystems. Although testing biotic agent responses to full plant VOC mixtures is ecologically more realistic, it leads to a far more difficult experimental approach to determine the relative importance of cues in an injured plant's VOC bouquet. Yet testing biotic agent (including plant) dose responses to blends may help to decipher VOC informational content [44, 45].

## Abbreviations

VOCs – volatile organic compounds  
 HIPVs – herbivore-induced plant volatiles  
 GLVs – green leaf volatiles  
 (Z)-3-hexenal – (Z)-3-HAL  
 (E)-2-hexenal – (E)-2-HAL  
 (Z)-3-hexenol – (Z)-3-HOL  
 (E)-2-hexenol – (E)-2-HOL  
 (Z)-3-hexen-1-yl acetate – (Z)-3-HAC  
 (Z)- $\beta$ -ocimene – (Z)-OCI  
 linalool – LIN  
 benzyl acetate – BAC  
 methyl salicylate – MAT  
 $\beta$ -caryophyllene –  $\beta$ -CAR  
 (E)- $\beta$ -farnesene –  $\beta$ -FAR

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