

VARIATION OF VOC EMISSIONS OF OAK TREES INFESTED BY OAK PROCESSIONARY MOTH

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Abstract

Herbivorous insects can cause severe damage to plants but simultaneously trigger distinct defense-related signaling pathways in the plant resulting in enhanced chemical defense. Here, we analyzed the effect of infestation with the oak processionary moth (*Thaumetopoea processionea* L., OPM) on volatile organic compound (VOC) emissions of oak leaves (*Quercus robur* L.). Variance of emitted VOCs and their correlations changed considerably under infestation., in particular in view of green leaf volatiles. Emissions of two alkanes (pentadecane and hexadecane) significantly increased in response to infestation. These VOCs possess known functions as semiochemicals that can convey a message from one plant to another and influence the behavior of the recipient.

2. Keywords: VOC; emission; oak; *Quercus robur* L.; oak processionary moth; *Thaumetopoea processionea* L.; green leaf volatiles; alkanes; pentadecane; hexadecane

3. Key Message: The volatile organic compound emissions of oak leaves (*Quercus robur* L.) infested with oak processionary moth (*Thaumetopoea processionea* L.) differ from non-infested trees in view of green leaf volatiles and two alkanes.

4. Introduction

More than 1.700 different volatile organic compounds (VOCs) which are produced and emitted by the various plant families of angio- and gymnosperms have been identified (Knudsen et al. 2006). Besides isoprene, monoterpenes and sesquiterpenes the quantitatively most important volatiles released by plants, also short-chained oxygenated compounds such as green leaf volatiles are emitted. VOCs fulfill many important ecological functions including communication between plants and animals (Farmer 2001; Dicke and Baldwin 2010; Francke and Dettner 2005; Gossner et al. 2014; Heuskin et al. 2011). Most importantly they serve as signal substances (infochemicals) in the interaction between plants and insects (Reddy and Guerrero 2004; Klaschka 2011). For example VOCs trigger insects to find host plants ensuring development of the offspring (Renwick 1989). Therefore, herbivores may use such infochemicals to distinguish between well and less well defended plants (Bonello et al. 2001).

Plant species release characteristic VOC patterns into the atmosphere, which can be driven by abiotic and biotic factors (Dindorf et al. 2006; Llusià et al. 2011). It has been shown that herbivore feeding can affect the composition and quantity of VOCs emitted by plants. For example, herbivory by the caterpillars *Tortrix viridana* L. and *Lymantria dispar* L. on *Quercus robur* L. considerably enhanced the emission of green leaf volatiles (Ghirardo et al. 2012; Copolovici et al. 2017) and monoterpenes (Copolovici et al. 2017). It is assumed that changed VOC emission in response to herbivore feeding can serve as both intra- and interspecific signals for other plant individuals leading to preparation and induction of plant defense mechanisms (Kost and Heil 2006; Frost et al. 2007; Heil and Bueno 2007).

Infestation of oaks by the oak processionary moth (*Thaumetopoea processionea* L., OPM), a native species in Germany, can cause severe damages on trees up to total defoliation (Groenen and Meurisse 2012; Sobczyk 2014). OPM population has been observed to increase and spread to northern latitudes most likely as a result of climate change (Groenen and Meurisse 2012). It's liable for this thermophilic moth to benefit from global warming and changing environmental conditions; consequently, mass outbreaks have to be expected to occur more frequently in future (Meurisse et al. 2012). Nonetheless, oak trees have an enormous regenerative capacity and single defoliation events are not expected to damage trees on a longer term. However repeated feeding by OPM over several years may lead to depletion of tree reserves, reduction of growth and vitality and an increased susceptibility to infestation by secondary pests and other stress factors (e.g., drought) (LWF 2018). In addition, OPM can cause serious problems to human and animal health as larvae of caterpillars develop stinging hairs that contain a nettle toxin (thaumetopoein). These stinging hairs trigger skin and eye irritation (contact dermatitis) as well as irritation of the respiratory tract (causing asthma) when they are dispersed with the wind (Bundschuh and Gerber 2014).

Here, we investigated the effects of naturally occurring OPM feeding activity on the VOC emission of leaves from adult pedunculate oak trees. We hypothesized that damages caused by OPM infestation will alter the composition of VOCs emitted from leaves., with particular changes of green leaf volatiles and other semiochemicals release.

5. Material and Methods

5.1. Field sites

The effects of the oak processionary moth (*Thaumetopoea processionea* L., OPM) on leaf-VOC-emissions of oak (*Quercus robur* L.) were studied on 12 non-infested trees and 14 infested trees in the cultural landscape of the Westhavelland in the meadowland Havellaendisches Luch in the Federal state of Brandenburg, Germany. Oak stands grow on sandy soils with contact to groundwater at riversides or downhill at (summer-) dry moraines. Trees were ~70 years old and had an average height of ~21 m.

5.2. Volatile sampling and identification

VOCs were collected in May 2017 using a modified dynamic enclosure system as described by Haberstroh et al. (2018). The mean air temperature during the sampling was 19°C while weather was sunny and windless. Selected twigs (with three to six leaves) were placed in custom-made glass enclosures (200 mm x 35 mm) with an outlet for VOC sampling. Each enclosure was sealed to the twigs with the odorless polyethyleneterephthalat-foil, Nalophan (Kalle, Wiesbaden, Germany) according to Rachow et al. (2012) and connected to an air sampling pump (210-1003MTX, SKC, Germany) through the outlet and via perfluoroalkoxy (PFA) tubes (Figure 1). For VOC sampling adsorbent tubes filled with polydimethylsiloxane (PDMS) foam (Gerstel GmbH & Co. KG, Germany) were installed between the glass enclosure outlet and the air sampling pump. The pump provided a controlled air flow (200 ml min⁻¹), which was passed over the adsorbent during the measurement for two hours accumulating VOCs from 24 l air flushing through each enclosure. Background VOC levels were determined from ambient air sampled at the same time next to the experimental trees.

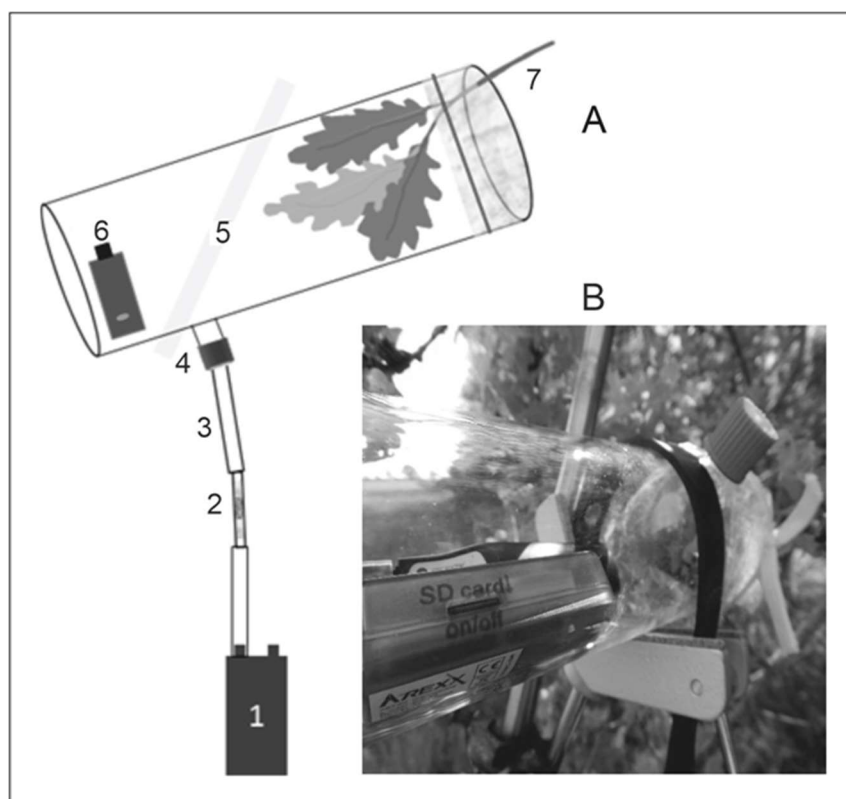


Figure 1: Dynamic enclosure system used for VOC emission analysis: (A) schematic view: 1 = pump; 2 = PDMS adsorbent; 3 = perfluoroalkoxy tube; 4 = enclosure outlet; 5 = glass enclosure; 6 = data logger; 7 = twig. (B) Photograph: Annett Reinhardt.

Analyses of the VOC samples were performed according to Haberstroh et al. (2018) using a gas chromatograph (GC model 7890A, Agilent Technologies Böblingen., Germany) connected to a Mass-Selective Detector (MSD 5975C, Agilent Technologies Böblingen., Germany) equipped with a thermodesorption-cold injection system (TDU-CIS, Gerstel, Germany). For VOC separation we used the same set-up and method as given by Haberstroh et al. (2018). VOCs were

identified using the program ChemStation (Version D 02.00.275, Agilent Technology, USA) and the mass spectral library from the National Institute of Standards and Technology (NIST MS Search 2.0., Gaithersburg, USA) (for an exemplary presentation of Total Ion Chromatograms, see Figure 2).

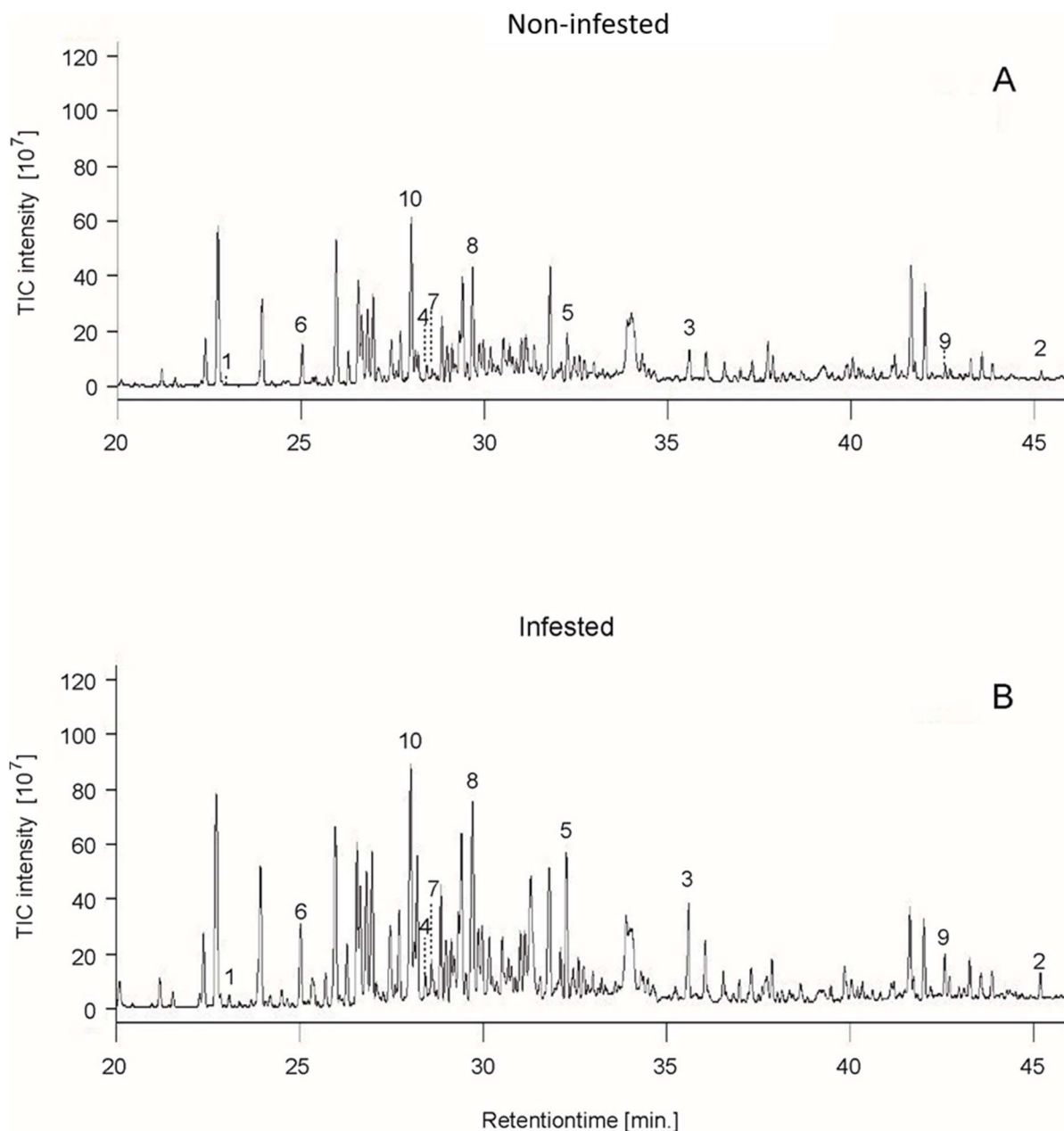


Figure 2: Exemplary chromatograms indicating Total Ion Count (TIC) of volatiles released from (A) non-infested oaks and (B) oaks infested by OPM. 1: pentadecane; 2: hexadecane; 3: decanal; 4: nonanal; 5: octanal; 6: α -pinene; 7: limonene; 8: 2-ethyl-1-hexanol; 9: (Z)-3-hexen-1-ol; 10: (Z)-3-hexenyl acetate.

5.3. Statistical analysis

Statistical analyses were performed using R 4.1.1 (R Development Core Team 2021). Variance and correlations of VOCs emitted from non-infested vs. infested oaks have been studied using Principal Component Analyses (PCA, varimax rotation) to ordinate variables and to identify the structure of relationships between these variables. In particular we wanted to identify the smallest number of factors that could account for the total variance that is to extract PCA-axis which are constructed from the variables and are most correlated. Thereby, the first PCA-axis accounts for the greatest amount of variation in the data matrix by maximizing the strongest co-variation among variables and the eigenvalues represent the proportion of original variance corresponding to a particular axis. Mann-Whitney-U-tests were used to compare the medians of the two independent VOC samples. This test is constructed by combining the two samples, sorting the data from smallest to largest, and comparing the average ranks of the two samples in the combined data.

6. Results

Overall, ten volatile compounds were detected to consistently occur in all samples: two alcohols ((Z)-3-hexen-1-ol, 2-ethyl-1-hexanol), one ester ((Z)-3-hexenyl acetate), two monoterpenes (limonene, α -pinene), three aldehydes (nonanal, decanal, octanal) and two alkanes (pentadecane, hexadecane). Ordination of VOCs from non-infested vs. infested oak trees are shown in Figure 3. The PCAs for non-infested and infested trees did only negligibly differ in the amount of total variation explained (88% vs. 90 %, respectively), but they differed in the structure of the relationship between variables. Non-infested oak leaves emitted a VOC-bouquet of seven substances: nonanal, decanal, octanal, (Z)-3-hexen-1-ol and (Z)-3-hexenyl acetate as well as pentadecane and hexadecane on the first axis (53% explained variance) and a bouquet of three substances: limonene, α -pinene and 2-ethyl-1-hexanol on the second axis (35% explained variance). In contrast, in infested oaks most of the variance of VOC-emissions was explained by limonene, α -pinene and 2-ethyl-1-hexanol on the first axis (47% explained variance), while a second and a third axis was characterized by a bouquet of nonanal, decanal and octanal as well as pentadecane and hexadecane (29% explained variance) and a bouquet of (Z)-3-hexen-1-ol and (Z)-3-hexenyl acetate (15% explained variance), respectively. Significant differences of VOC-abundances between the medians of non-infested and infested oaks were found for the two alkanes pentadecane ($p = 0.025$) and hexadecane ($p = 0.015$) with higher values in infested oaks (Figure 4).

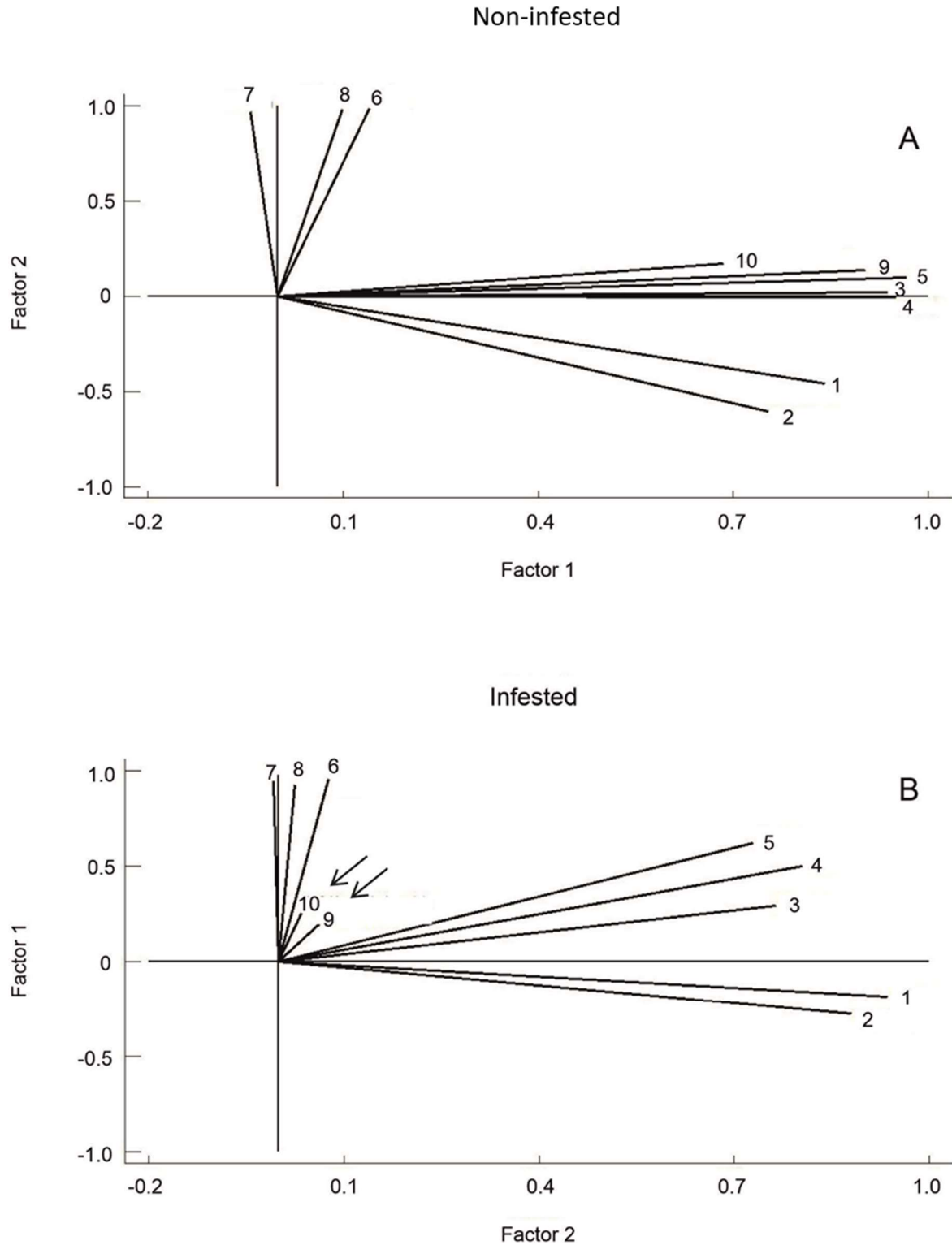


Figure 3: Results of a Principle Component Analysis (PCA). Ordinations of ten VOCs in (A) non-infested oaks and (B) oaks infested by OPM. 1: pentadecane; 2: hexadecane; 3: decanal; 4:

nonanal; 5: octanal; 6: α -pinene; 7: limonene; 8: 2-ethyl-1-hexanol; 9: (Z)-3-hexen-1-ol; 10: (Z)-3-hexenyl acetate.

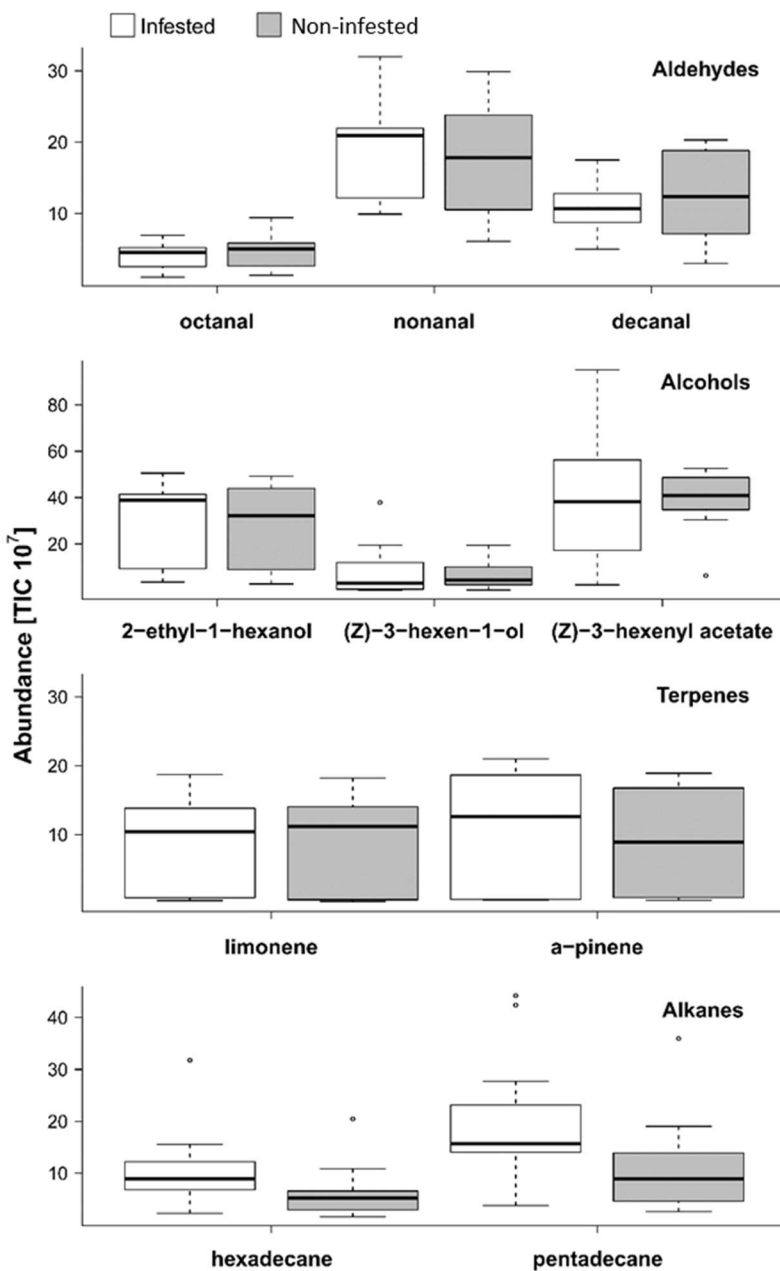


Figure 4: Box-and-Whisker Plots of ten VOCs with minima (0th percentile), first quartiles (25th percentiles), medians (50th percentiles), third quartiles (75th percentiles) and maxima (100th percentiles).

7. Discussion

In the present work., we investigated the impact of infestation with the oak processionary moth (OPM) on the emission of VOCs from oak leaves. The analyses showed that the relative frequency

distribution of VOCs differs distinctly between non-infested and infested oaks for the green leaf volatiles (GLVs) 2-ethyl-1-hexanol, (Z)-3-hexen-1-ol and (Z)-3-hexenyl acetate gaining importance in the course of OPM infestation. To the best of our knowledge, the high relative importance of GLVs presented here appears to be the first evidence for their involvement in plant defense mechanisms in oaks infested by OPM. Particularly, the relative changes of (Z)-3-hexen-1-ol and (Z)-3-hexenyl acetate complement the picture of signal-VOCs within and between plants and as multifunctional weapon against herbivores and pathogens (Matsui 2006; Scala et al. 2013). Since GLVs are released as a result of mechanical damage and/or plant stress as a consequence of plasma membrane disruption (Hatanaka 1993; Fall et al. 1999; Porta & Rocha-Sosa 2002), they may be expected to function as signals for other organisms in the oak environment. GLV may repel or attract herbivores and their natural enemies, induce plant defense mechanisms or prime plants for enhanced defense against herbivores and pathogens and have direct toxic effects on bacteria and fungi (Turlings et al. 1991; Engelberth et al. 2004; Scala et al. 2013; Ameye et al. 2015; Ameye et al. 2018). To test such plant-plant interaction mediated by GLV emission, the defense capacity of non-infested oak leaves growing very close to infested leaves should be studied in future.

On the other hand the monoterpenes limonene and α -pinene were emitted by oak leaves. Earlier studies suggested that limonene might act as a repellent against herbivorous insects (Nordlander 1990; Martini et al. 2010) and to be toxic to bark beetles even at low concentrations (Reid and Purcell 2011; Chiu et al. 2017). In addition, both monoterpenes are known to attract natural enemies of herbivores (Zhang et al. 2009; Alhmedi et al. 2010; Mohammed et al. 2020). It still has to be investigated if these compounds have similar functions for oak defense against the OPM.

Fluctuations of abiotic and biotic stress factors may influence the release of VOCs under different environmental conditions (Ameje et al. 2018). For aldehydes such as nonanal, decanal and octanal our study revealed that these volatiles occurred to a significant extent in both infested and non-infested oaks. Aldehydes like nonanal and octanal are known to attract natural enemies such as Coleoptera, Hemiptera, Hymenoptera and Syrphidae (de Groot 2003; James 2005; Yu et al. 2008) and therefore may be of general importance for plant defense against insect herbivores. In contrast the abundance of two alkanes: pentadecane and hexadecane was significantly higher in infested oaks. These long-chain hydrocarbons are components of plant leaf waxes (Li and Ishikawa 2006; Sarkar et al. 2013; Karmarkar et al. 2016; Mitra et al. 2017; Das et al. 2019) and might act as attractants for herbivorous insects (Karmarkar et al. 2016; Mitra et al. 2017; Mitra et al. 2020).

8. Conclusion

In conclusion oaks emit VOCs that may play a role in attracting OPM and other potential pest insects. For example, oaks in mixed forests are said to be less heavily infested by OPM than oaks in monocultural forests (Damestoy et al. 2020). Identifying of these host location signals may contribute to a better understanding of OPM-outbreaks. Oaks also emit VOCs as results to

herbivore feeding. These GLV either mediate direct plant defense (e.g., because of their toxicity), they might communicate a warning signal to leaves of the same tree or neighboring trees or attract the pest's natural enemies thereby contributing to biological pest control strategies. Biological pest control becomes increasingly important. Oak forest management could further promote and benefit from forest diversification and naturally occurring enemies.

Author contribution statement

JK., CT., AMA: data analysis; AR: field experiment., data collection., created method figure; AMA: project advisor. All of the authors collaborated on writing the text and revision.

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Declarations

Conflict of interest

The authors declare that they have no conflict of interest.

Consent for publication

All the authors have read and agreed to the published version of the manuscript.

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