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Phytochemistry 66 (2005) 1540–1550
PHYTOCHEMISTRY
www.elsevier.com/locate/phytochem

How rainfall, relative humidity and temperature influence volatile emissions from apple trees in situ

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Received 14 December 2004; received in revised form 20 April 2005
Available online 9 June 2005

Abstract

Headspace volatiles from apple-bearing twigs were collected in the field with a Radiello sampler during three different diurnal periods over the complete fruit growing season. Analyses by thermal desorption–GC–MS identified a total of 62 compounds in changing quantities, including the terpenoids α-pinene, camphene, β-pinene, limonene, β-caryophyllene and (*E*,*E*)-α-farnesene, the aldehydes (*E*)-2-hexenal, benzaldehyde and nonanal, and the alcohol (*Z*)-3-hexen-1-ol. The variations in emission of these plant odours were statistically related to temperature, humidity and rainfall in the field. Remarkably, rainfall had a significant positive influence on changes in volatile release during all three diurnal periods, and further factors of significance were temperature and relative humidity around noon, relative humidity in the late afternoon, and temperature and relative humidity during the night. Rainfall was associated consistently with an increase in the late afternoon in terpene and aldehyde volatiles with a known repellent effect on the codling moth, one of the key pests of apple fruit. During the summer of 2003, a season characterized by below-average rainfall, some postulated effects of drought on trees were tested by establishing correlations with rainfall. Emissions of the wood terpenes α-pinene, β-pinene and limonene were negatively correlated with rainfall. Another monoterpene, camphene, was only detected in this summer but not in the previous years, and its emissions were negatively correlated with rainfall, further supporting the theory that drought can result in higher formation of secondary metabolites. Finally, the two green leaf volatiles (*E*)-2-hexenal and (*Z*)-3-hexen-1-ol were negatively correlated with rainfall, coinciding well with the expectation that water deficit stress increases activity of lipoxygenase. To our knowledge, this work represents the first empirical study concerning the influence of abiotic factors on volatile emissions from apple trees in situ.

Keywords: *Malus domestica* Borkh.; *Lepidoptera Tortricidae*; *Cydia pomonella*; Apple tree; Abiotic factors; Temperature; Relative humidity; Rainfall; Volatiles; Plant stress

1. Introduction

Chemical changes in plants in response to changing environmental conditions have intrigued experts in chemistry, ecology and food science. Variation in emitted plant odours can be triggered by a changing biotic environment such as herbivore feeding (reviewed by Karban and Baldwin, 1997; Dicke and van Loon, 2000; Mattiacci et al., 2000), or by varying abiotic factors such as temperature and humidity (Takabayashi et al., 1994; Gouinguené and Turlings, 2002). Altered chemical emissions can influence interactions with organisms in the environment of the plant, resulting for example in a modified susceptibility to insects and pathogens (Hildebrand, 1989). Changes in the composition of secondary metabolites can in the case of an agricultural crop such as apple, have a significant influence on the flavour (Schmitz-Eiberger et al., 2003). While variations due to biotic factors, in particular induction

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0031-9422/$ - see front matter © 2005 Elsevier Ltd. All rights reserved.
doi:10.1016/j.phytochem.2005.04.038

of volatile release by herbivore insects, have been studied intensively (e.g. Boevé et al., 1996; Hern and Dorn, 2001), relatively little information is available on how abiotic conditions affect odour emissions.

Abiotic conditions and subsequent volatile releases from plants may be subject to dramatic changes during a diurnal cycle (Loughrin et al., 1994). Temperature and humidity were shown to influence the composition of released blends significantly, even in perennial plants. In the pine, *Pinus halepensis* L., monoterpene emission rate increased with temperature at different humidities, while temperature had only an impact at high humidity in the oak, *Quercus ilex* L. (Llusià and Peñuelas, 1999). These experiments were carried out with potted plants under standardized indoor conditions, similarly as those with the slash pine, *Pinus elliottii* Engelm., where monoterpene emissions increased again with temperature, and light had no direct effect (Tingey et al., 1980).

Water deficit stress is known as a further key abiotic factor influencing plant metabolism profoundly. It alters carbon allocation between roots and shoots (Teskey et al., 1987) and changes nutrient uptake ratios and nutrient circulation (Schulze, 1991), with major implications on volatile emissions and ecology (Takabayashi et al., 1994). In potted apple plants grown under largely controlled conditions in the greenhouse, water deficit stress increased the emission of volatiles with a chain length of *n*-C_6-carbons (Ebel et al., 1995).

Laboratory and greenhouse studies are ideal frames for factorial experiments, but they provide incomplete information with respect to the complex situations and interactions found in the field. Potted plants, for example, have a limited soil volume surrounding the rhizosphere, hence even experimental designs to study water deficit stress require relatively frequent irrigation to avoid complete desiccation of the plants. Furthermore, rainfall cannot be optimally simulated by soil irrigation, as the leaves remain dry instead of being wetted by drops of water falling on them over a certain period of time. Finally, the response of plants in the field may be subject to combined influences of several environmental variables, including temperature, relative humidity and rainfall.

This study aims at addressing this gap in knowledge by investigating the influence of the abiotic factors, temperature, relative humidity, and rainfall on the emission of volatiles from the apple tree (*Malus domestica* Borkh.) in situ. The volatile profiles from the headspace of fruit-bearing twigs with leaves will be analysed in total, with special emphasis on the terpenes and aldehydes which are important constituents of apple volatiles (Takabayashi et al., 1994; Hern and Dorn, 2002) and can have a behavioural effect on leptidopteran herbivore insects of the apple tree. One of the most serious pests of apple worldwide, the codling moth *Cydia pomonella* L. (Lepidoptera, Tortricidae) (Dorn et al., 1999), utilises odours from apple trees in search for oviposition sites (Yan et al., 1999; Hern and Dorn, 2002). The moth flies towards the host tree in the evening while no movements are observed at noon (Bovey, 1966). Mated females are attracted to the dosages of some terpenes as they are emitted from healthy apples, including (*E*,*E*)-α-farnesene (Hern and Dorn, 1999), limonene and β-caryophyllene, while they are repelled by β-pinene and the aldehydes nonanal and benzaldehyde (Vallat and Dorn, 2005). In the field in late August, emissions from ripening apple fruit were found to be neither attractant nor repellent for approaching female codling moths (Hern and Dorn, 2002). All these findings together indicate that changing compositions of volatile blends emitted from the apple plant might result in contrasting behavioural responses of this herbivore pest insect, and that the influence of abiotic conditions might play an important role in this ecological context.

Starting from volatile collections carried out over the complete growing season and during three different diurnal periods, statistical methods were applied to evaluate the effect of humidity, temperature and rainfall on the profiles of volatiles and on components known for their bioactivity on the codling moth. To our knowledge, this work represents the first empirical study concerning the influence of abiotic factors on volatile emission from apple trees under field conditions.

2. Results and discussion

2.1. Seasonal changes in volatile emissions

Overall, 62 volatile compounds were identified in the headspace of apple fruit-bearing twigs with leaves, among them 9 terpenoids and 10 aldehydes (Tables 1 and 2). The 10 compounds printed in bold are discussed in more detail below; all of them are apple constituents and most of them are behaviourally effective on the codling moth. Volatile emissions in situ changed significantly over the growing season 2003 (ANOVA repeated measures: $F = 147.202$, $P < 0.0001$). Emissions from three individual apple trees used for volatile collection did not differ significantly (ANOVA repeated measures: $F = 0.865$, $P > 0.05$). Furthermore, no significant interaction was found between individual apple trees and the sampling dates (ANOVA repeated measures: $F = 0.788$, $P > 0.05$).

The marked seasonal dynamics of volatile emission observed in summer 2003, with two maxima of overall emissions measured in early June and mid August, coincide well with the results of a previous study that focused on apple fruit only and that was carried out in summer 1998 (Hern and Dorn, 2003). Altered biotic conditions such as infestation by codling moth larvae