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Instantaneous and historical temperature effects on α -pinene emissions in *Pinus halepensis* and *Quercus ilex*

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Abstract

We compared the role of instantaneous temperature and temperature history in the determination of α -pinene emissions in Mediterranean conifer *Pinus halepensis* that stores monoterpenes in resin ducts, and in Mediterranean broad-leaved evergreen *Quercus ilex* that lacks such specialized storage structures. In both species, α -pinene emission rates (E) exhibited a significant exponential correlation with leaf temperature and the rates of photosynthetic electron transport ($J_{CO_2+O_2}$) started to decrease after an optimum at approximately 35°C. However, there was a higher dependence of E on mean temperature of previous days than on mean temperature of current day for *P. halepensis* but not for *Q. ilex*. $J_{CO_2+O_2}$ showed a maximum relationship to mean temperature of previous 3 and 5 days for *P. halepensis* and *Q. ilex* respectively. We conclude that although the best correlation of emission rates were found for instantaneous foliar temperatures, the effect of accumulated previous temperature conditions should also be considered in models of monoterpene emission, especially for terpene storing species.

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Introduction

Biogenic Volatile Organic Compounds (BVOCs) are produced and emitted by many plant species and have a series of relevant physiological and ecological functions (Peñuelas and Llusia, 2001, 2004). Emission of these compounds has also major consequences for ambient air quality. In particular, these plant-generated compounds can react rapidly with anthropogenic and biogenic trace components of atmosphere (e.g. OH radical, ozone and NO₃ radical) and contribute to tropospheric ozone and photochemical smog formation, thereby significantly curbing the quality of ambient air (Atkinson, 2000; Chameides *et al.*, 1988; Fehsenfeld *et al.*, 1992). In addition, BVOCs might play an important role in altering the climate at regional and global scales (Penuelas and Llusia, 2003; Kulmala *et al.*, 2004; Tunved *et al.*, 2006). Because of

potentially important role of BVOC in tropospheric air quality and climate, there is continuous interest in developing BVOC emission models to quantify plant-generated volatile flux over large areas (Guenther *et al.*, 1993, 1995, 2006; Niinemets *et al.*, 2002; Martin *et al.*, 2000; Arneth *et al.*, 2007).

Some monoterpene-emitting species like needle-leaved conifers all across the world and many odorous species in Mediterranean macchia have specialized tissues such as resin ducts or glandular trichomes for storage of produced volatile isoprenoids. On the contrary, some other strong monoterpene-emitting species like Mediterranean evergreen oaks such as *Quercus ilex* L. do not have specific storage tissues for monoterpenes (Llusia and Penuelas, 2000; Loreto *et al.*, 1996a). These anatomical differences are

important as the terpenoid emission from specialized storage is expected to depend only on the diffusion from the storage pools, while in the species lacking the storage pools, the emission is mainly driven by the immediate rate of synthesis (Fall, 1999; Kesselmeier and Staudt, 1999; Niinemets *et al.*, 2004).

The rate of terpene emission (E) strongly depends on environmental conditions, in particular, on instantaneous leaf temperature (Penuelas and Llusia, 2001, 2003; Atkinson 2000; Kesselmeier and Staudt, 1999; Ozkan, 2009; Tingey *et al.*, 1980). Typically, the emission rates depend exponentially on temperature, and such an exponential dependence of emissions on instantaneous temperature has been implemented in all terpene emission models. Currently, plant terpene emissions are mostly predicted using Guenther *et al.* algorithm (G93 model (1993). For species with specialized storage structures, this model simulates the emission rates using a species-specific basal emission rate (E_0) and scaling the values of E_0 to different temperatures according to an exponential relationship (the temperature correction factor). For monoterpene-emitting species lacking storage structures, isoprene emission algorithm (Guenther *et al.*, 1993) that uses additionally light as an emission driver has been implemented (Bertin *et al.*, 1997; Ciccioli *et al.*, 1997).

Recently, complementary modeling approaches have been developed that use plant physiological properties to predict emissions (Martin *et al.*, 2000; Niinemets *et al.*, 1999; Zimmer *et al.*, 2000). For instance, the rate of monoterpene emission in species lacking specialized storage structures has been predicted on the basis of photosynthetic electron transport rate ($J_{CO_2+O_2}$) and monoterpene synthase activity (Niinemets *et al.*, 2002). Monoterpene synthase activity provided an estimate of basal emissions analogous to E_0 (fraction of electrons in monoterpene synthesis on the model), while $J_{CO_2+O_2}$ that depends on instantaneous environmental variables, temperature and photosynthetic photon flux density, was used to scale the basal emissions to different temperature and light conditions (Niinemets *et al.*, 2002). In other physiological models, the emission were also linked to photosynthetic carbon metabolism in various ways (Martin *et al.*, 2000; Niinemets *et al.*, 1999; Zimmer *et al.*, 2000; Bäck *et al.*, 2005). It has been stated that such modeling approaches allow consideration of stress effects on volatile isoprenoid emissions (Grote and Niinemets, 2008). For example, stress-dependent reductions in $J_{CO_2+O_2}$ are suggested to explain the rapid decline in monoterpene emissions in stressed plants (Niinemets *et al.*, 2002).

E_0 values were initially supposed to be constant and represent the inherent plant capacity for production of a particular volatile compound (Winer *et al.*, 1992; Seufert *et al.*, 1995; Karlik and Winer, 2001). However, it has become increasingly apparent that the basal emission rates can change over time (Llusia and Penuelas, 2000; Kuhn *et al.*, 2004; Gray *et al.*, 2003, 2006; Goldstein *et al.*, 1998), but the factors controlling such temporal modifications are still poorly understood. Furthermore, the available emission algorithms have mainly focused on the influence of instantaneous leaf temperature on

the emission rates and $J_{CO_2+O_2}$. However, many plant physiological processes are known to strongly acclimate to previous leaf temperature environment (Yamori *et al.*, 2005; Huve *et al.*, 2006; Bauerle *et al.*, 2007), and temperature history likely alters terpene emission rates as well. Already Schumann (1993) suggested that in some plants, the monoterpene emission may involve distinct long-term kinetic mechanisms. It has been further suggested that isoprene basal emission rate is altered by leaf thermal history (Sharkey *et al.*, 1999; Fuentes and Wang, 1999; Geron *et al.*, 2000; Lehning *et al.*, 2001; Petron *et al.*, 2001), but the way plant emissions adjust to leaf temperature environment is not fully understood. While it has been suggested that leaves respond to average temperature of previous days (Sharkey *et al.*, 1999; Fuentes and Wang, 1999; Geron *et al.*, 2000; Lehning *et al.*, 2001; Petron *et al.*, 2001), it is also not clear over what time period ambient leaf temperatures alter leaf emissions. Given that the internal pool sizes are much larger in species with specialized storage structures, it is expected that the emissions respond to longer historical temperature signal in species with specialized storage structures than in species lacking such storage structures in the foliage.

The aim of the present study was to evaluate the relative importance of instantaneous temperature and temperature history in determining α -pinene emissions in monoterpene-storing Mediterranean evergreen conifer *Pinus halepensis* Mill. and in Mediterranean evergreen broad-leaved species *Quercus ilex* L. that lacks specialized monoterpene storage tissues. Emissions were monitored during the entire season simultaneously with leaf environmental conditions and the correlations of E and $J_{CO_2+O_2}$ with instantaneous temperatures and with average temperature over different number of days prior to measurements were determined to assess the strength of instantaneous and historical temperature signals.

Materials and Methods

Plant material: Full experimental details and the protocol for α -pinene emission measurements are provided in Blanch *et al.* (2007). In short: the experiment was conducted in the campus of the Universitat Autònoma de Barcelona, Catalonia, Spain (41°29' N, 2°6' E, elevation 147 m) throughout the summer of 2004. Two-year-old potted (2 l. pots) seedlings of *Pinus halepensis* (seedling source: Apromi breeding ground, Juneda, Lleida, Spain) and *Quercus ilex* (seedling source: Forestal Catalana, Breda, Girona, Spain) were used for the experiments. The plants were grown outside under typical Mediterranean conditions in an open plastic tunnel. The plants were watered every two days up to soil field capacity, giving an equivalent of 1 l. of water per week and pot.

α -Pinene emission rates in *Pinus halepensis* and *Quercus ilex* were measured every 6 days over the growing season. Instantaneous leaf temperatures and incident quantum flux densities were measured during the emission measurements, while mean daily temperatures were obtained from a climatic station in the locality of the study. The α -pinene emission measurements were conducted at the leaf-level: one leaf of *Q. ilex* and one shoot of *P. halepensis*

were clamped in the cuvette, the emission measurements were conducted using an ADC gas exchange system: we divided the output flow tube using a T-system: a part of the flow went into a new tube, in which we placed a three-bed carbon trap tube, and a pump at the end, so, the output air from the cuvette was forced to pass through the carbon tube at a controlled flow (with the pump). In order to subtract the outgoing monoterpenes from the ingoing air stream and in order to consider the carry-over effect of the cuvette we made one blank sample every 3 samples: we sampled one cartridge with the cuvette closed without clamping any shoot or leaf. Moreover, we waited 10 minutes between each sample with the cuvette opened in order to get the system ventilated.

Estimation of photosynthetic electron transport rate ($J_{CO_2+O_2}$): The photosynthetic electron transport rate ($J_{CO_2+O_2}$, $\mu\text{mol m}^{-2} \text{s}^{-1}$) needed to achieve a rate of net carbon assimilation A ($\mu\text{mol m}^{-2} \text{s}^{-1}$) was calculated as (Brooks and Farquhar, 1985):

$$J_{CO_2+O_2} = \frac{(A + R_d)(4C_i + 8\Gamma^*)}{C_i - \Gamma^*}$$

where R_d is rate of mitochondrial respiration continuing in the light ($\mu\text{mol m}^{-2} \text{s}^{-1}$), Γ^* ($\mu\text{mol mol}^{-1}$) is the hypothetical CO_2 compensation point in the absence of R_d (Laisk, 1977) and C_i is the intercellular CO_2 concentration ($\mu\text{mol mol}^{-1}$).

R_d is estimated from the proportionality between A and R_d observed at 25°C ($R_d = 0.15 A$). Γ^* at different leaf temperatures was estimated according to Lambers *et al.* (1998), using the following equation:

$$\Gamma^* = \Gamma_{25}^* + 0.0188(T-25) + 0.0036(T-25)^2$$

where Γ_{25}^* is constant (3.7 Pa).

Measurement of average temperature of previous days: Average temperature of days preceding the measurements T_n ($n = 1-15$) was calculated as:

$$T_n = \frac{\sum_{d=1}^{d=n} T_d}{n}$$

where n is the number of days preceding the measurements and T_d is the average daily air temperature corresponding to day d .

Statistical analyses: In both species, correlations between E and $J_{CO_2+O_2}$ and averages of temperature were calculated with different number of days prior to measurements, starting with the mean temperature of the day of sampling (T_1) and ending with the mean temperature of the 15 days preceding the measurements (T_{15}).

The effects of leaf temperature and mean temperature of previous days (T_n , Eq. 4) on the instantaneous α -pinene emission rates (E) were analyzed by exponential regressions. The effects of leaf temperature and mean temperature of previous days (T_n , Eq. 4) on the rate of photosynthetic electron transport ($J_{CO_2+O_2}$)

were analyzed by quadratic regressions (adjust to a 2nd grade polynomial).

All the statistical analyses were performed with R 2.7.2 for Windows (R Foundation for Statistical Computing, Vienna, Austria).

Results and Discussion

The emission rates of α -pinene in *P. halepensis* range from 1.3 to 19.8 $\mu\text{g g}^{-1} \text{h}^{-1}$ and those of *Q. ilex* between 0.11 and 14.7 $\mu\text{g g}^{-1} \text{h}^{-1}$. E exhibited a significant positive exponential correlation with leaf temperature during the measurements in both species, *P. halepensis* ($r = 0.64$, $p < 0.001$) and *Q. ilex* ($r = 0.57$, $p < 0.001$) (Fig. 1). $J_{CO_2+O_2}$ showed a significant quadratic correlation with leaf temperature in *P. halepensis* ($r = 0.59$, $p < 0.01$) but not in *Q. ilex* (Fig. 2).

The storing species *P. halepensis* showed an increase of the correlation coefficient of α -pinene emission rates with mean temperature of previous days when considering increasing number of days, reaching the highest correlation coefficient with the mean temperature of the previous 13 days (T_{13} , Fig. 3).

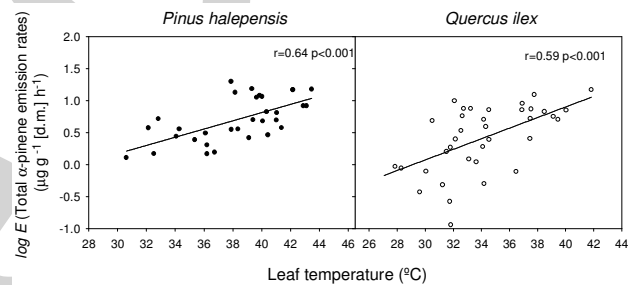


Fig. 1: Relationships between α -pinene emission rates (E) and leaf temperature in evergreen conifer *Pinus halepensis* and evergreen broad-leaved tree *Quercus ilex*. Each datapoint corresponds to a separate leaf. Data were fitted by exponential regressions

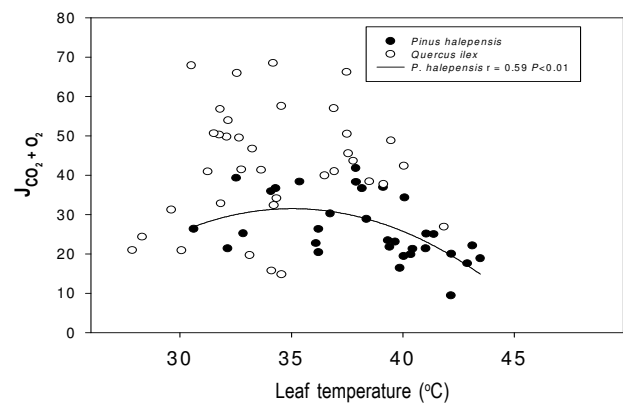


Fig. 2: Relationships between the rate of photosynthetic electron transport ($J_{CO_2+O_2}$) and leaf temperature in evergreen conifer *Pinus halepensis* and evergreen broad-leaved tree *Quercus ilex*. Each datapoint corresponds to a separate leaf. Data were fitted by quadratic regressions. $J_{CO_2+O_2}$ values are expressed per unit projected leaf area in both species

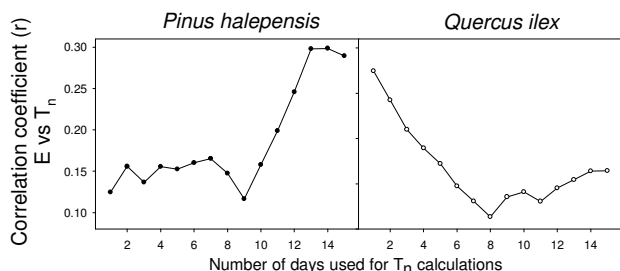


Fig. 3: Correlation coefficient (r) of α -pinene emission rate (E) with the historical average temperature (T_n) while varying the number of days for calculation in *P. halepensis* and *Q. ilex*. The number of days ranged from 1 (mean temperature of the day of sampling) until 15 (mean temperature of the preceding 15 days). The maximum values correspond to T_{13} ($r = 0.29$, $p < 0.1$) for *P. halepensis* and T_1 ($r = 0.27$, $p < 0.1$) for *Q. ilex*

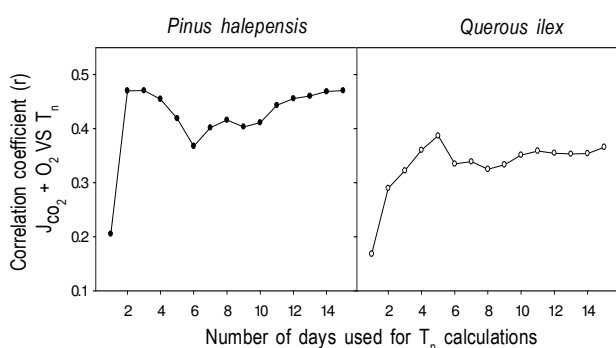


Fig. 4: Correlation coefficient (r) of the rate of photosynthetic electron transport ($J_{CO_2+O_2}$) with the historical average temperature (T_n) while varying the number of days for calculation in *P. halepensis* and *Q. ilex*. The number of days ranged from 1 (mean temperature of the day of sampling) until 15 (mean temperature of the preceding 15 days). The maximum values correspond to T_3 ($r = 0.47$, $p < 0.05$) for *P. halepensis* and T_5 ($r = 0.39$, $p < 0.1$) for *Q. ilex*

The non-storing species *Q. ilex* did not show any improvement of the correlation coefficient with previous days for E (Fig. 3). On the contrary, the best correlation was found with the mean temperature of the day of sampling (T_1 , Fig. 3, $r = 0.27$, $p < 0.1$).

The correlation coefficient of $J_{CO_2+O_2}$ with mean temperature of previous days increased from the first to the following previous days reaching a maximum at the mean temperature of the three previous days for *P. halepensis* ($r = 0.47$, $p < 0.05$) and at the mean temperature of the five previous days for *Q. ilex* (Fig. 4, $r = 0.39$, $p < 0.1$).

Previous studies have generally reported lower total monoterpene emission rates for *P. halepensis*. Alessio et al. (2004) found emissions of α -pinene of $0.4 \mu\text{g g}^{-1} [\text{d.m.}] \text{h}^{-1}$, Ormeno et al. (2007) found emissions between 0.5 and $1.2 \mu\text{g g}^{-1} \text{h}^{-1}$, and Penuelas and Llusia (1999) found emissions of $1.5 \mu\text{g g}^{-1} [\text{d.m.}] \text{h}^{-1}$. However, our data was collected in a Mediterranean ecosystem during the high temperatures of the Mediterranean summer in a range between 30 and 44°C . High precaution was taken while conducting the measurements to avoid clamping damage of the needles.

Regarding the α -pinene emission rates of *Q. ilex*, our data (0.11 to $14.7 \mu\text{g g}^{-1} \text{h}^{-1}$) agrees with previous studies. Alessio et al. (2004) found emissions of $1.7 \mu\text{g g}^{-1} [\text{d.m.}] \text{h}^{-1}$, Street et al. (1997) found emissions between 2.5 and $3 \mu\text{g g}^{-1} [\text{d.m.}] \text{h}^{-1}$, Owen et al. (Owen et al., 1997) reported α -pinene emissions rates between 0.5 and $20 \mu\text{g g}^{-1} [\text{d.m.}] \text{hr}^{-1}$ and Llusia and Penuelas (2000) found maximum α -pinene emissions of $5 \mu\text{g g}^{-1} [\text{d.m.}] \text{hr}^{-1}$.

Both species, *P. halepensis* and *Q. ilex* showed high correlation coefficients (r) of α -pinene emission rates (E) with instant leaf temperature (0.64 and 0.59 respectively, Fig. 1), as it was expected. It has been widely reported that monoterpene emission rates depend exponentially on instantaneous temperatures (Atkinson 2000; Penuelas and Llusia, 2003; Kesselmeier and Staudt, 1999; Tingey et al., 1980).

The Arrhenius-type curve describing the dependence of $J_{CO_2+O_2}$ on instant temperatures in both species (Fig. 2) indicates that the measurements were done around the maximum $J_{CO_2+O_2}$ of the plant, which supports the high values of α -pinene emissions. Because of that, there were also some measurements that were conducted above the maximum and therefore those plants could have suffered photoinhibition due to the high temperatures.

Terpene emissions in a terpene-storing species such as *P. halepensis* are expected to rely mainly on the extensive storage pools, and are thus, believed to be less sensitive to rapid modifications in the rate of terpene synthesis, for instance, after changes in light (Guenther et al., 1993; Tingey et al., 1991). The increase of the correlation coefficients of E from T_1 to T_{13} (Fig. 3) indicates that the pools of monoterpenes depend more on the historical temperature of previous days than of the current day.

The emissions of α -pinene in non-storing species such as *Q. ilex* are on the contrary directly dependent on the rate of terpene synthesis (Fall, 1999), that can be altered by temperature, light and water availability (Loreto et al., 1996b; Staudt and Seufert, 1995; Kesselmeier et al., 1996). Consequently, the emissions of non-storing species are more dependent on the temperature and light conditions in the day of sampling than on the mean temperature of previous days (Fig. 3). These weaker correlation of E with historical temperature may reflect the importance of the initial rapid change in the emission potentials as outlined by Hanson and Sharkey (2001).

In both species *P. halepensis* and *Q. ilex* there was evidence of previous days adjustment in $J_{CO_2+O_2}$ that was completed after three and five days respectively (Fig. 3). Given that $J_{CO_2+O_2}$ may partly control terpene emission rate through NADPH and ATP availability for terpene synthesis (Ninemetts et al., 2002), such long-term changes may reflect coupled adjustment in $J_{CO_2+O_2}$, for instance through anatomical adjustments such as modifications in chloroplast to total leaf surface area ratio (Oguchi et al., 2003; 2005) or modifications in nitrogen investment in the components of photosynthetic machinery and in enzymes controlling terpene synthesis (e.g. Hikosaka et al., 1999). It has been observed that

acclimation in the heat-stability of photosynthetic electron transport takes between 5-7 days in deciduous trees (Huve *et al.*, 2006).

The best correlations of emission rates were found for instantaneous foliar temperatures, partly explaining the success of simple empirical models based on temperature response such as the Guenther model (Guenther *et al.*, 1993), but overall, these data also underscore the importance of previous leaf temperature environment in determining monoterpene emission rate, in particular in species with extensive foliar monoterpene reservoirs. There have been attempts to include such adaptation responses in the volatile isoprenoid emission models (Guenther *et al.*, 2000), but species-specific variation in the previous environmental signal and environmental signals of various time length have, to our knowledge, not been considered. The effect of accumulated previous day conditions should thus be considered and implemented in modeling of volatile isoprenoid emissions.

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