Changes in terpene content and emission in potted Mediterranean woody plants under severe drought

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Abstract: Terpene concentration and emission were studied in potted plants of some of the most common Mediterranean woody species (Pinus halepensis L., Pistacia lentiscus L., Cistus albidus L., Cistus monspeliensis L., Quercus ilex L., Quercus coccifera L., Phillyrea latifolia L., Phillyrea angustifolia L., and Arbutus unedo L.) under irrigation and under severe drought conditions that dropped relative water content to a range between 40% in Q. ilex and 85% in Phillyrea latifolia after withholding watering for one dry summer week. Terpene concentrations were detected in Pinus halepensis, Pistacia lentiscus, C. albidus, and C. monspeliensis, and they increased after withholding watering except in C. albidus. Terpene emission was detected in all species except Phillyrea angustifolia and A. unedo. Pinus halepensis showed the highest diurnal terpene emission rates of 86 μg·g⁻¹ dry wt·h⁻¹ followed by C. albidus, Pistacia lentiscus, Q. ilex, Q. coccifera, Phillyrea latifolia, and C. monspeliensis (4 μg·g⁻¹ dry wt·h⁻¹). Emitted terpenes represented from 0.33% of C fixed in C. monspeliensis to 10% in C. albidus. All species severely decreased their terpene emission rates under severe drought conditions. Emission by terpene-storing species (e.g., Pinus halepensis) was more related to temperature than in nonstoring species (e.g., Q. ilex), which showed emission relationships with photosynthetic rates. The monoterpene α-pinene, β-pinene, β-phellandrene, and limonene and the sesquiterpene caryophyllene were the most abundant terpenes stored and emitted by these Mediterranean plant species.

Key words: drought, Mediterranean conditions, terpene concentration, terpene emission, woody plants.

Résumé : Les auteurs ont étudié la teneur et l’émission de terpènes chez les plantes en pot de quelques espèces méditerranéennes les plus communes, Pinus halepensis L., Pistacia lentiscus L., Cistus albidus L., Cistus monspeliensis L., Quercus ilex L., Quercus coccifera L., Phillyrea latifolia L., Phillyrea angustifolia L. et Arbutus unedo L. sous irrigation et sous l’effet de sécheresse poussée ayant amené la teneur relative en eau dans une fourchette allant de 40% chez le Q. ilex à 85% chez le Phillyrea latifolia après avoir retenu l’arrosage pendant une sèche semaine d’été. Des teneurs en terpènes ont été décelées chez les Pinus halepensis, Pistacia lentiscus, C. albidus et C. monspeliensis, et ces teneurs augmentent après l’omission de l’eau, sauf chez le C. albidus. L’émission de terpènes a été perçue chez toutes les espèces sauf chez les Phillyrea angustifolia et A. unedo. Le Pinus halepensis a montré les taux d’émission diurnes en terpènes les plus élevés avec 86 μg·g⁻¹ poids sec·h⁻¹ suivi des C. albidus, Pistacia lentiscus, Q. ilex, Q. coccifera, Phillyrea latifolia et C. monspeliensis (4 μg·g⁻¹ poids sec·h⁻¹). Les terpènes émis représentent de 0,33% du C fixé chez le C. monspeliensis à 10% chez le C. albidus. Toutes les espèces voient leurs taux d’émission en terpènes diminuer fortement sous des conditions de sécheresse sévère. L’émission de terpènes par les espèces qui les accumulent (e.g., Pinus halepensis) était plus reliée à la température que chez les espèces qui ne les accumulent pas (e.g., Q. ilex), lesquelles montrent des relations entre l’émission et les taux photosynthétiques. Les monoterpènes α-pinènes, β-pinènes, β-phellandrene et limonène, et le sesquiterpène caryophyllène sont les terpènes accumulés et émis en plus grandes quantités par ces plantes méditerranéennes.

Mots clés : sécheresse, conditions méditerranéennes, teneur en terpènes, émission de terpènes, plantes ligneuses.

Introduction

Production and emission of terpenes are influenced by several biotic and abiotic factors (Peñuelas and Llusia 1997). Water availability is one of the most important abiotic fac-
sors. Terpene concentrations have been generally found to increase in drought conditions (Hodges and Lorio 1975; Gershenzon et al. 1978; Kämmlänen et al. 1991). On the contrary, terpene emissions may be reduced when the stress is severe. In a progressive drought, monoterpene emission has been found to drop when the daily CO₂ balance approached zero (Bertin and Staudt 1996).

Soil water availability represents a major environmental constraint under Mediterranean summer conditions (Di Castri 1973). It determines the cyclic pattern of vegetation activity together with air temperature and solar radiation. Currently, climatic studies of the Mediterranean region in northeastern Spain have shown a trend of increasing temper-
ature and drought in recent years relative to first part of the century (Piñol et al. 1998). Global change effects on Mediterranean climate are likely to provide even more and stronger droughts such as the recent ones of 1986 and 1994 in Mediterranean Spain (Houghton et al. 1996, Peñuelas 1996). It is likely that the warmer and drier weather and droughts will persist in the future with the possibility of having significant effects on vegetation, including their terpene concentration and emission. To test the effect of drought, we measured terpene concentration and emission of nine typical Mediterranean potted woody plants (Pinus halepensis L., Pistacia lentiscus L., Cistus albidus L., Cistus monspeliensis L., Quercus ilex L., Quercus cocifera L., Phillyrea latifolia L., Phyllirea angustifolia L., and Arbutus unedo L.) under increasing severe drought conditions produced by withholding irrigation.

Materials and methods

Experimental conditions

The experiment was conducted with 2-year-old seedlings of Pinus halepensis, Pistacia lentiscus, C. albidus, Phillyrea latifolia, Q. ilex, Q. cocifera, C. monspeliensis, A. unedo, and Phyllirea angustifolia growing in 1.8-L pots filled with a fine-textured natural soil. They were grown inside a plastic tunnel 28 m long and 6 m wide to avoid undesired watering by natural precipitation. From 10 June 1996 onwards, 20 plants of each species were irrigated once per day to maximum pot capacity (1 L) and watering of 20 other plants was withheld until 17 June. Photosynthetic rates, stomatal conductances, and terpene sampling were conducted in the morning (07:00–09:00 solar time), at midday (12:00–13:00 solar time), and in the evening (16:00–17:00 solar time) on Q. ilex, Pistacia lentiscus, Q. cocifera, and Phillyrea latifolia. All the other species were only measured at 09:00 and 17:00 because of lack of time.

Gas exchange and terpene sampling and analysis

Leaf net photosynthetic rate and stomatal conductance were determined with a portable gas exchange system (ADC4, configured with chamber model PLC-2P, ADC Inc., Hoddesdon, Hertfordshire, England). Lateral branch ends with several leaves were inserted into the chamber. Special attention was devoted to avoid leaf damage, which was never evident. There was, thus, no apparent disturbance in terpene storage structures of terpene-storing species that could have explained the high emission rates (Juuti et al. 1990). Three plants per species and sampling time were measured.

Sampling of terpene emission was conducted simultaneously with the measurement of CO₂ and H₂O exchange. Intact leaves were clamped in a Parkinson chamber (PLC-2) adapted to the ADC-LCA-4. A T system was used for terpene sampling. Air coming out of the cuvette flowed through the T system to a glass tube (11.5 cm long and 0.4 cm internal diameter) filled with terpene adsorbents Carbotrap C (300 mg), Carbotrap B (200 mg), and Carboisve S-III (125 mg) from Supelco (Bellefonte, Pa.) separated by plugs of quartz wool. The tubes hydrophobic properties minimized sample displacement by water and avoided transformation of terpenes as checked with standards. These tubes were previously conditioned for 3 min at 350°C with a stream of purified helium. The sampling time was 3 min, and the flow varied between 100 and 200 mL min⁻¹ depending on the glass tube. The flow for each tube was determined with a bubbler's flowmeter. The terpene trapping efficiency was virtually 100%. To eliminate the problem of "sticky" terpenes adsorbed by the surfaces and materials used in the gas exchange system, free air flowed for 15 min, and a blank with no branch in the gas exchange system was sampled immediately before each measure. The glass tubes (with trapped terpenes) were stored into a portable fridge at 4°C and taken to the laboratory. The glass tubes were then stored at −20°C before analysis (no longer than 24–48 h later). There were no observable changes in terpene concentrations after storage of the tubes.

For extraction of leaf terpenes, several fully developed leaves were cut; submerged in pentane, stored in the portable fridge at 4°C; taken to the laboratory, where they were homogenized in Teflon tubes with a Teflon pestle; and stored at −30°C until analysis (not longer than 48–72 h later). An internal standard (dodecane) was used to quantify recovery of extracted terpenes (they were larger than 90%).

Terpene analyses were conducted in a gas chromatograph—mass spectrometer (GC–MS; Hewlett Packard HP5982B, Palo Alto, Calif.). Trapped emitted monoterpenes were desorbed (Thermal Desorption Unit, model 890/891; Supelco, Inc., Bellefonte, U.S.A.) at 320°C during 3 min and injected into a 30 m × 0.25 mm × 0.25 mm film thickness capillary column (Supelco HP-5, cross-linked 5% PhMe silicone). After sample injection, the initial temperature (46°C) was increased to 30°C min⁻¹ up to 70°C and, thereafter, at 10°C min⁻¹ up to 150°C; this temperature was maintained for 5 min. Helium flow was 1 mL min⁻¹. The identification of monoterpenes was confirmed using the GC–MS by comparison with standards from Fluka (Chemie AG, Buchs, Switzerland), literature spectra, and GC-Derivatization Chemstation G1074A HP. An internal standard (dodecane) together with frequent calibration with standards (once every three analyses) were used for quantification. Calibration curves were always highly significant (r² > 0.99). For most of the studies, these techniques showed a good reproducibility in the measured emission rates and relative composition of terpenes produced by different leaves of the same species.

Statistical analyses

All statistical analyses (analyses of variance (ANOVA's), correlations, and regression models) were conducted using SYSTAT, version 5.2 (SYSTAT Inc., Evanston, Ill.) and StatView, version 4.5 (Abacus Concepts Inc., Berkeley, Calif.) statistical program packages. Three plants per treatment (treatment and control) were measured each time for each species. Data were log transformed to meet normality requirements. ANOVAs were conducted for all studied species together and for each one separately and also for total terpenes and for each one separately.

Results

Terpene concentrations and emissions

Terpene concentrations were detected only in four of the nine studied species (Pinus halepensis, Pistacia lentiscus, C. albidus, and C. monspeliensis) and ranged between 1.55 μg g⁻¹ dry wt. in C. monspeliensis and 2753 μg g⁻¹ dry wt. in Pinus halepensis under irrigated conditions. After irrigation was withheld, terpene concentration increased approximately 45% in Pinus halepensis and Pistacia lentiscus, and approximately 90% in C. monspeliensis (Fig. 1). It did not change in C. albidus.

Pistacia lentiscus had the largest number of individual terpenes followed by Pinus halepensis (Fig. 1, Table 1). The most abundant terpene in Pistacia lentiscus and Pinus halepensis was α-pinene. Cistus monspeliensis stored only α-pinene in the irrigated treatment and α-pinene, caryophyllene, and α-caryophyllene in the drought treatment, and C. albidus stored only caryophyllene (Fig. 1, Table 1). Thus, the monoterpenes α-pinene, β-pinene, β-phellandrene, and limonene and the sesquiterpenes caryophyllene and α-caryophyllene were the most abundant terpenes stored by these Mediterranean species.
Fig. 1. Individual terpene concentration and emission rates of the studied terpene-storing species under irrigated and drought conditions. (*, p < 0.01, ANOVA for drought treatment; n = 6–9 for terpene emission in each treatment and species corresponding to two or three times daily measurements). b, bicyclo[3.1.0]hexane, 4-methylene-1-(1-methylethyl) -. Errors bars are 95% confidence limits. Notice that emission rates were so small in the drought treatment that most of them are not visible in the figure.

Terpene emission was detected in seven of the nine studied species (Pinus halepensis, Pistacia lentiscus, C. albidus, Q. ilex, Phillyrea latifolia, C. monspeliensis, and Q. coccifera). Phillyrea angustifolia and A. uvedo did not emit detectable terpenes. Daily average total terpene emission rates ranged between 3.59 µg·g⁻¹ dry wt·h⁻¹ in C. monspeliensis and 85 µg·g⁻¹ dry wt·h⁻¹ in Pinus halepensis in irrigated conditions (Fig. 1). After withholding watering there was no emission of terpenes except for very small amounts in Pistacia lentiscus and C. monspeliensis.

Pinus halepensis emitted α-pinene, β-pinene, Δ²-carene, β-myrcene, α-phellandrene, and camphene, and P. lentiscus emitted α-pinene, α-phellandrene, ν-limonene, β-pinene, and β-myrcene. Cistus albidus emitted caryophyllene, Δ²-carene, camphene, and α-pinene; Q. ilex emitted α-pinene, limonene, β-pinene, and camphene. In C. monspeliensis, we only detected α-phellandrene; in Q. coccifera, only limonene and α-pinene; and in Phillyrea latifolia, ν-limonene, α-pinene, and β-pinene (Figs. 1 and 2, Table 1). Thus, these emitted terpenes did not always coincide with the stored terpenes. For example, α-phellandrene was emitted by C. monspeliensis even though it did not store it in detectable amounts (Fig. 1, Table 1).

Daily patterns in photosynthetic photon flux density (PFD), temperature, photosynthetic rate, stomatal conductance, and terpene emission

During the daily sampling period (07:00–17:00, solar time), the PFD inside the branch chamber showed maxima around 1300 µmol·m⁻²·s⁻¹ at midday and minima of approximately 400 µmol·m⁻²·s⁻¹ in the evening, and chamber air temperatures varied between 25 and 40°C (Fig. 3). Temperatures, like PFD, showed a typical daily cycle with maximum temperature at noon in all cases.

The photosynthetic rate had the typical summer Mediterranean maximum in the morning in the species for which a daily cycle was studied, such as Q. ilex and Pistacia lentiscus. As expected, drought-stressed plants showed the lowest values including negative net photosynthetic rates (from −1.35 in Q. coccifera to −0.06 in Q. ilex), when respiration was higher than photosynthesis (negative values in Fig. 3). Leaf stomatal conductance showed a similar behaviour, with higher values (30–79 mmol·m⁻²·s⁻¹) in irrigated plants than in drought-stressed plants, which showed very low stomatal conductances (between 0 and 15 mmol·m⁻²·s⁻¹) showing very severe water deficits (Fig. 3).
Table 1. Average percentage of stored and emitted terpene compounds by *Pinus halepensis*, *Pistacia lentiscus*, *Quercus ilex*, *Quercus cocifera*, *Phillyrea latifolia*, *Cistus albidus*.

<table>
<thead>
<tr>
<th>Terpene</th>
<th>Stored (%)</th>
<th>Emitted (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td>α-Pinene</td>
<td>17</td>
<td>4</td>
</tr>
<tr>
<td>β-Pinene</td>
<td>14</td>
<td>2</td>
</tr>
<tr>
<td>A-β-Carene</td>
<td>14</td>
<td>3</td>
</tr>
<tr>
<td>l-Myrcene</td>
<td>15</td>
<td>2</td>
</tr>
<tr>
<td>α-Phellandrene</td>
<td>9</td>
<td>1</td>
</tr>
<tr>
<td>β-Limonene</td>
<td>4.3</td>
<td>0.3</td>
</tr>
<tr>
<td>Caryophyllene</td>
<td>8</td>
<td>3</td>
</tr>
<tr>
<td>Bicyclo[3.1.1]Hex-2-ene</td>
<td>3</td>
<td>0.3</td>
</tr>
<tr>
<td>4-methylene-1,5-cyclohexadiene</td>
<td>0.3</td>
<td>0.1</td>
</tr>
<tr>
<td>α-Phellandrene-2-Carene</td>
<td>4</td>
<td>1</td>
</tr>
</tbody>
</table>

Fig. 2. Individual terpene emission rates of the studied nonstoring species under irrigated and drought conditions (*, p < 0.01, ANOVA for drought treatment; n = 6–9 for each treatment and species corresponding to two or three times daily measurements). Errors bars are 95% confidence limits. Notice that emission rates were so small in the drought treatment that most of them are not visible in the figure.

Total emitted terpenes were maximal in the morning (around 09:00) in irrigated *Q. ilex* (89 ± 5.2 μg·g⁻¹ dry wt·h⁻¹) and then decreased (12 ± 1.9 μg·g⁻¹ dry wt·h⁻¹ at 17:00) (Fig. 4). *Pistacia lentiscus* had a maximum terpene emission rate at 12:00 (45 μg·g⁻¹ dry wt·h⁻¹) and, thereafter, decreased only slightly (35 μg·g⁻¹ dry wt·h⁻¹ at 17:00) (Fig. 4). *Quercus cocifera* also showed a maximum terpene emission rate at 12:00 (19 μg·g⁻¹ dry wt·h⁻¹) and was greatly decreased at 17:00 (0.45 μg·g⁻¹ dry wt·h⁻¹). In species that stored terpenes like *Pinus halepensis*, there was a significant log-linear correlation of terpene emission rates with temperature (r = 0.77, p < 0.05), whereas in species not storing terpenes like *Q. ilex*, terpene emission was significantly log-linearly correlated with the assimilation rate (r = 0.45, p < 0.05) but not with temperature (Fig. 5).

**Discussion**

**Concentration and emission in different species**

Some of the studied Mediterranean plant species stored and emitted appreciable amounts of terpenes (*Pinus halepensis*, *Pistacia lentiscus*, *C. albidus*, and *C. monspeliensis*), and others (*Q. ilex*, *Q. cocifera*, and *Phillyrea latifolia*) emitted significant amounts of terpenes even though they did not store terpenes in detectable amounts. Two of the nine studied species (*Phillyrea angustifolia* and *A. unedo*) did not appreciably store nor emit terpenes.
Fig. 3. Diurnal cycle of photosynthetic photon flux density (PFD), leaf temperature, photosynthetic rate, and stomatal conductance for *Q. ilex* and *P. lentiscus* in irrigated and drought conditions (*n* = 3 for each treatment, time, and species). Error bars are ± 1 SE.

The monoterpenes α-pinene, β-pinene, α-phellandrene, and limonene and the sesquiterpene caryophyllene were the most abundant terpenes stored and emitted by the studied Mediterranean plants. This study, therefore, shows that some species such as *Q. ilex*, *Phillyrea latifolia*, and *Q. coccifera* may be emitters of terpenes without containing (storing) them, as has been demonstrated for *Q. ilex*, which was found to emit large amounts of monoterpenes (Hewitt and Street 1992; Staadt and Seufert 1995; Loreto et al. 1996a, 1996b). Results for *Phillyrea latifolia* also coincide with data presented previously by Hewitt and Street (1992) who found that the species emits terpenes at a lower rate than *Q. ilex*. Results for *A. unedo*, which had no detectable terpene content nor emission, do not agree with a previous study (Owen et al. 1997), which found a significant emission rate of several terpenes. Studies with more sensitive detection will have to be conducted with this species.

Fig. 4. Diurnal cycle of total monoterpe, α-pinene, β-pinene, and limonene emission rates for *Q. ilex* and *P. lentiscus* in irrigated and drought conditions (*n* = 3 for each treatment, time, and species). Error bars are ± 1 SE.

The measured emission rates are some of the highest emission rates ever measured for terpene emission (Guenther et al. 1994). Plants storing terpenes normally have specialized structures (ducts and glands). This is the case for *Pinus halepensis* and *Pistacia lentiscus*. Even though careful attention was paid to avoiding disturbance of terpene storage structures, it is not certain that they were completely undamaged. Nevertheless, although *Q. ilex* does not store terpenes, and therefore, there was no possible damage to storage structures, it was also an important emitter compared with these terpene-storing plants. In these plants, although emitted terpenes did not always coincide with stored terpenes, the degree of coincidence was high (Fig. 1, Table 1). Schindler and Kotzias (1989) also found that the internal composition of monoterpenes in needles and twigs of conifers sometimes did not reflect the composition of released volatiles.
Responses to severe drought

In the terpene-storing species (Pinus halepensis, Pistacia lentiscus, C. monspeliensis, and C. albidus), content and emission responded differently to drought treatment. This drought treatment was severe. It dropped the relative water content to a range between 40% in Q. ilex and 85% in Phillyrea latifolia (Filella et al. 1998). The concentrations of terpenes under drought conditions were higher than in irrigated conditions (except in C. albidus). Total terpene concentrations of Pinus halepensis, Pistacia lentiscus, and C. monspeliensis exposed to drought conditions increased by 26.5, 21.3, and 92.5%, respectively, in comparison with controls under irrigated conditions. These results are also in agreement with previous data showing that water stress alters terpene leaf concentrations. For example, water deficit induced an increase in terpene concentrations in Pinus taeda L. (Hodges and Loirio 1975) and in Picea abies (L.) Karst. (Kainulainen et al. 1991). In Satureja douglasii (Benth.) Briq., populations, changes in leaf water potential from −6 to −9 bars (1 bar = 100 kPa) were accompanied by significant increases in terpene concentrations, from 17 to 21 mg g⁻¹ of dry leaf weight (Gershenzon et al. 1978). In general, under moderate water stress, plants accumulate carbon because of growth restriction by water limitation. It is assumed that this carbon may then be allocated to defense (protection) compounds such as monoterpenes, storage, or to wood (Bradford and Hsiao 1982; Peñuelas and Estiarte 1998).

Emission was very inhibited by the severe drought conditions produced by withholding watering as has also been found in other studies (Bertin and Staudt 1996; Loreto et al. 1996b). These results are useful in understanding the behaviour of plant volatiles in Mediterranean conditions during summer, which is important because of their flammability in forest fires (Philpot and Mutch 1971) or because of their role in atmospheric chemistry processes favoring ozone formation (Thompson 1992). Thus, drought stress could lead to a large overestimation of the emission under summer conditions, because the algorithms based only on light and temperature would give too high emissions rates (Bertin and Staudt 1996).

Emission relations with temperature and photosynthetic rates

In species containing terpenes, like Pinus halepensis, monoterpenes emission rates increased in a log-linear relationship with temperature (Fig. 5). This indicates an exponential increase of terpene emission with the increase in temperature. Studies of Pinus elliottii Engelm. (Tingey et al. 1980), Salvia mellifera Greene, and Mentha xipiperita L. (Tingey et al. 1991) have shown that temperature strongly affects emission. Even for nonstoring species such as Q. ilex, Loreto et al. (1996b) found that α-pinene emission increased three times when temperature increased from 20 to 30°C.

There were significant correlations of total terpene emission rates with net photosynthetic rates in nonstoring species such as Q. ilex suggesting that these two processes increase together. As Q. ilex does not store terpenes, the emitted monoterpenes must have been synthesized recently (Staudt and Seufert 1995). Terpene emission rates of nonstoring species such as Q. ilex or Phillyrea latifolia in irrigated conditions represented 5.35 and 1.09%, respectively, of fixed carbon, i.e., they were higher but of the same order of magnitude as the percentage found by Loreto et al. (1996b) for Q. ilex (2.5%). The high emission rates could be linked to an ongoing very active monoterpen metabolism as suggested by Staudt and Seufert (1995). It has been recently shown that monoterpen formation seems to be dependent on ATP availability (Loreto et al. 1996a) and that monoterpen precursors originate from photosynthetic activity (Loreto et al. 1996a, 1996b). Curiously, Q. cocifera and Pistacia lentiscus, among others, emitted terpenes under negative net
photosynthetic rates indicating that, even in such drought-stress conditions, part of the photosynthetic C fixation is used for terpene production and emission. However, the emission rates dramatically decreased in all nonirrigated plants, which is in agreement with dramatic decreases in net photosynthetic rates and stomatal conductances. Numerous studies of leaf gas exchange in Mediterranean-type climates, including studies in potted trees, have shown similar leaf responses to those described here of decreasing net photosynthetic rates and stomatal conductances with increasing drought (Tenhunen et al. 1990; Peñuelas et al. 1998).

There was a low correlation between emission rate of monoterpenes and stomatal conductance that can be explained by the lack of control of stomata over the emission. Terpenes that are stored internally appear to exit the leaves through stomata, but stomatal conductance apparently has little effect on emission rate (Lerdau 1991). However, in our measurements the stomatal closure (Fig. 3) could help to explain the absence of terpene emission in most of studied species in severe drought conditions.

Conclusions

The terpene-storing species were found to increase their terpene concentration and to decrease their terpene emission under drought conditions. The terpene emission of non-storing species also dramatically decreased after the severe water stress. α-Pinene was the most abundant terpene emitted by Pinus halepensis, Pistacia lentiscus, and Q. ilex. Phellandrene was the only monoterpenes emitted by C. monspeliensis, whereas carpyphylene was the most important in C. albidus, and limonene, in Q. cocifera and Philyrea latifolia. Terpene emission rates ranged between 0.33% of the carbon fixed in C. monspeliensis and 10% in C. albidus.

All these results should be considered in prediction algorithms, inventories, and modelling of monoterpenes, which mostly do not consider the general increase in content and the high decrease in terpene emission under drought stress. This is especially important in ecosystems such as the Mediterranean ones, where the studied species are common.

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