

***Interactive comment on “Drought reduced
monoterpene emissions from *Quercus ilex* trees:
results from a throughfall displacement
experiment within a forest ecosystem” by
A. V. Lavoit et al.***

A. V. Lavoit et al.

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We thank referee 2 for the comments on our manuscript. We will consider them carefully and try to answer at best. Please find our statement below.

1. “ The message of the paper is not clear. It is concluded that drought negatively affects monoterpene emission, and that drought reduces the overall flux of monoterpenes from Mediterranean forests. The second allegation (e.g. last sentence of the abstract) is not supported by experimental results and may only be advanced as a speculation. ”

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We partially agree with this comment. Our study only deals with *Quercus ilex* species; inferring our results on Mediterranean evergreen forest might be speculative. To be more precise, we suggest replacing "Mediterranean evergreen forest" (in the abstract p. 865) and "Mediterranean oak forest" (in the conclusion p. 882) by "Mediterranean Holm oak forest".

2. "But I have problems also with the first conclusion, as some results do not clearly show a negative effect of drought on monoterpene emission. For instance, when data in control and drought stressed plots are compared in Fig. 1 (emission) and 3 (standard emission) no clear evidence of an effect of drought can be seen."

In the present manuscript we demonstrate data from a field experiment designed to manipulate soil water uptake during 2 growing seasons. Indeed, in both years precipitation was so low that differences between normal natural drought ("control") and additional "drought"; plots were masked by an overall occurring drought stress situation. The difference of plant water status between these two treatments was comparable significantly different. Therefore, and because monoterpene emission rates responded non-linearly to drought, no statistically significant difference between the mean emissions rates of the normal drought and additional drought treatment could be seen (p. 880, l. 18-29). Nevertheless a clear influence of water limitation was observed: (i) Via a drastic drop of monoterpene emissions accompanied by a cessation of foliar gas exchange in summer when climatic conditions (light and temperature) were stable and optimal for emission process. These periods corresponded exactly to the periods of severe drought, as described by the plant and soil water status indexes (p. 877, l. 6-10). (ii) Via a significant difference between the irrigated plot and others which were submitted to natural or accentuated drought.

3. "When standard emission from the irrigated plot is compared with the other two plots (Fig. 4 and 3), the emissions of the 2005 drought-stressed samples appear to be similar to those of the irrigated plot."

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Measurement periods were slightly moved back in 2006 (May to December) compared to 2005 (April to September) (p. 869, l. 23-24). In 2005, emission reached maximal values in spring and decreased in summer. In 2006, on the irrigated plot, monoterpene emissions increased in spring, were maximal in summer and decreased in fall.

4. "I think that the authors should re-analyze their data, clearly stating what Fig. 5, and the overall data-set, probably reveal; monoterpene biosynthesis and emission are relatively insensitive to drought when this is mild, or even rather heavy (see abstract 14-16), but monoterpene biosynthesis and emission drop when the stress reaches a threshold. This is reminiscent of what has been observed with isoprene, the other volatile hydrocarbon that is commonly emitted by trees. In a recent paper, Brilli et al. (New Phytol 2007) came across similar results with drought-stressed potted poplars, and concluded that a threshold of transpirable soil water exists after which isoprene is considerably inhibited. I think the results of this paper could valuably expand the indications of the paper by Brilli, which is not even mentioned in the current version. The existence of a threshold is mentioned in the discussion (page 880) but it should be brought about as the core result of this paper, and adequately supported with pertinent literature. The paper by Brilli also offers a valuable insight of alternative carbon sources for terpenes in drought-stressed leaves, while the two mentioned papers (page 882-11) do not directly refer to drought stress. "

I agree with the pertinence of the paper by Brilli et al. in this subject. In a revised version we will mention this work. Nevertheless, this paper was done on young potted poplar plants which were isoprene emitters and highly sensitive to drought. Moreover in Brilli et al. the plant water status was assessed by the relative soil water content whereas in our study by the pre-dawn plant water potential, which further limits a direct comparison of the results of these two studies.

5. " The paper unfortunately also shows several methodological problems and unclear writing. The emissions are clearly affected by a combination of effects, including seasonality, leaf age, and the attack of pests. Discrimination of the drought stress effect is

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attempted but not clear."

We do not agree with this comment, even when we are aware that dissection of field data is not trivial. However, in our opinion field measurements are necessary, because the drought response of plants growing in their natural multi-stress and competitive environment might be different to the response of plants kept under controlled growth conditions, and this is what our data actually indicate. In the manuscript we seriously discuss seasonality, leaf development, and pests attack and we removed them one by one to explain the observed variations of monoterpene emission (p.879).

6. "The data-set reduction to summer values in Fig. 5 should be justified more quantitatively than it has been done. In Fig. 5 legend, the data-set actually used for the plot is not even mentioned, and it appears that all data are plotted."

In Figure 5, all data (2005 and 2006, control and dry plots) except fall and spring measurements were plotted in order to avoid that drought effects are confounded with developmental and post-stress recovery effects. In our analysis, we focused on the "optimal period" for monoterpene emission in terms of temperature and light conditions, during which drought appeared (DOY 140-242 in 2005, DOY 150-235 in 2006). Within this period, we observed the water limitation effect under minimized influence of seasonality. However, we must not lose sight of the fact that under field conditions such an influence cannot be dissected completely.

7. "Many more data should be shown. The result section opens with a paragraph non of whose data is shown. Some of those data are of interest and should be shown. For instance it would be interesting to see that emissions reflect activation of corresponding enzymes. Is this true also in stressed leaves."

We agree with the interest of these results, but they did not directly contribute to the topic of this study. The paper is already long; we had to make a choice. The monoterpene patterns obtained by in vitro assays of mono-TPS activity were similar to those found in the emission measurements for stressed leaves (linear regression:

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$r^2=0.68$, Paired t-test: $P=0.999$, sigma plot) and for unstressed leaves (linear regression, $r^2=0.72$, Paired t-test: $P=0.999$, sigma plot).

8. "The coefficients for light and temperature-dependent correction of emission to calculate the standard emission should also be shown."

In a revised version of the manuscript we will add the values (p. 873): $\alpha=0.0041$; $CL_1=1.04$; $CT_1 = 87.62 \text{ J mol}^{-1}$; $CT_2=188200 \text{ J mol}^{-1}$; $TM=317 \text{ K}$; $TS=303 \text{ K}$

9. "Incidentally, the presentation of the determination of the standard emission is cumbersome and unclear (873)."

In a revised version we will try to describe the procedure of normalisation of monoterpene emission (p.873, l.18-28) more clearly and more shorten.

10. "For instance, it is speculated that photosynthesis drops earlier than monoterpene emission because of stomatal closure (page 882). How do we know? With the available data, calculation of intercellular CO_2 concentration should be possible."

Graph comparison pointed that photosynthesis dropped earlier than MT emissions (Fig. 3: DOY 190 in 2005 or DOY 150 in 2006). Actually, stomatal closure and intercellular CO_2 concentration are available but once again we could not show all data set. Stomatal closure showed the same seasonal variation than photosynthesis even during water stress periods. This result agreed with literature which considers that photosynthesis is limited by stomatal conductance in early stages of a drought stress period (e. G. Flexas et al 2002, 2004; Galmès et al 2007...). However, intercellular CO_2 concentration remained stable until the leaf water potential reached -3MPa . From this value, the fluorescence parameter started to decline, reflecting metabolic limitations.

11. "Data about the 2007 comparison between one-year and current-year leaves (879-10) should be shown."

Again, with a mind to lighten the paper, we did not present this result. It could be added

if necessary.

12. "Some other important references are missing and some are misquoted. For instance, the first paper addressing the possible role of drought stress on volatile terpenes (Sharkey and Loreto, *Oecologia* 1993) should be quoted on page 866. It is not true that all studies quoted on page 866 have been performed with young potted plants."

The mentioned paper of Sharkey & Loreto in 1993 is not the first paper addressing drought stress effects on isoprenoids. To our knowledge the first paper addressing this question is by Tingey et al. in 1981, showing effects of drought in isoprene emission in young-potted *Quercus virginiana* plants. We counted about thirty references on this subject (mainly on isoprene) and choose only a few for citation. The first one should effectively be quoted. Indeed, the paper by Loreto et al 2001 presented a study made on mature trees but in controlled conditions. This accuracy could be added.

13. "Some definitions are inexact and other are missing. For instance, reference to BVOC (page 865 and following) is misplaced here. The paper only deals with monoterpenes and this should be made clear since the very beginning."

BVOC reference allowed us to introduce the chemical impact of these compounds on the atmospheric chemistry and the matter of study dealing with the quality and the quantity of emitted compounds. These characters concern all the BVOC compounds, and particularly monoterpenes and isoprene which are preponderant. Similar reflection could concern the species of interest and an introductory reference to Mediterranean forests. We decided to introduce a general context and we focused on monoterpenes and *Quercus ilex* as a sample of this context.

14. "It is unclear what "basal emission rates - instantaneous emission rates"; are (866)."

"Basal emission rates" is defined as the intrinsic capacity of plant to emit biogenic com-

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pounds (at 30°C and 1000 mol m⁻² s⁻¹ PPDF) and the "instantaneous emission rates"; is the emission rate at a given time with given light and temperature conditions. To avoid misunderstanding we will replace "basal emission rates" by "standard emission factors" and "emission rates" as suggested in the M & M section (p. 873, l. 27-28).

15. "It is also unclear how weather effects on monoterpene emissions were minimized by the measurement routine (869-27)."

In our experimental design we decided to measure gas exchange and monoterpene emission under ambient conditions with given light and temperature values of the respective (sunny) days to take into actual account. Light and temperature were kept stable during the sampling period of cartridges for VOC analysis. Nevertheless, we are aware of the problem of diurnal variation of monoterpene emission (and even the diurnal variation of standard emission factors by circadian rhythms and diurnal turnover of metabolic intermediates). To minimize these influences the measurements were performed within a few hours around midday. Along these lines, seasonal variability of monoterpene emissions includes intrinsic seasonality and environmental factors (like cloudy weather). To compare emissions between seasons at best, measurements were made only under sun-lit conditions i.e. under optimal light conditions (also temperature) for a given season.

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