

Impacts of soil moisture on de-novo monoterpene emissions

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Impacts of soil moisture on de-novo monoterpene emissions from European beech, Holm oak, Scots pine, and Norway spruce

C. Wu¹, I. Pullinen¹, S. Andres¹, G. Carriero², S. Fares³, H. Goldbach⁴, L. Hacker¹, T. Kasal⁴, A. Kiendler-Scharr¹, E. Kleist⁵, E. Paoletti², A. Wahner¹, J. Wildt⁵, and T. F. Mentel¹

¹Institut für Energie und Klimaforschung, IEK-8, Forschungszentrum Jülich, 52425 Jülich, Germany

²Istituto Protezione Sostenibile Piante, Consiglio Nazionale Ricerche (CNR), Via Madonna del Piano 10, 50019 Sesto Fiorentino, Firenze, Italy

³Consiglio per la Ricerca e la sperimentazione in Agricoltura (CRA), Research Centre for the Soil–Plant System, Rome, Italy

⁴Department of plant nutrition, INRES, Universität Bonn, Karlrobert Kreiten Str. 13, 53115 Bonn, Germany

⁵Institut für Bio- und Geowissenschaften, IBG-2, Forschungszentrum Jülich, 52425 Jülich, Germany

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Correspondence to: J. Wildt (j.wildt@fz-juelich.de)

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Abstract

Impacts of soil moisture on de-novo monoterpene (MT) emissions from Holm oak, European beech, Scots pine, and Norway spruce were studied in laboratory experiments. The volumetric water content of the soil, Θ , was used as reference quantity to parameterize the dependency of MT emissions on soil moisture and to characterize the severity of the drought.

When Θ dropped from $0.4 \text{ m}^3 \text{ m}^{-3}$ to $\sim 0.2 \text{ m}^3 \text{ m}^{-3}$ slight increases of de-novo MT emissions were observed but with further progressing drought the emissions decreased to almost zero. The increases of MT emissions observed under conditions of mild drought were explainable by increases of leaf temperature due to lowered transpirational cooling. When Θ fell below certain thresholds, MT emissions decreased simultaneously with Θ and the relationship between Θ and MT emissions was approximately linear. The thresholds of Θ ($0.044\text{--}0.19 \text{ m}^3 \text{ m}^{-3}$) were determined as well other parameters required to describe the soil moisture dependence of de-novo MT emissions for application in the Model of Emissions of Gases and Aerosols from Nature, MEGAN.

A factorial approach was found appropriate to describe the impacts of Θ , temperature, and light. Temperature and Θ influenced the emissions largely independent from each other, and, in a similar manner, light intensity and Θ acted independently on de-novo MT emissions. The use of Θ as reference quantity in a factorial approach was tenable in predicting constitutive de-novo MT emissions when Θ changed on a time scale of days. Only when soil moisture changed suddenly empirical parameterization with Θ as a reference was unsuccessful.

1 Introduction

Biogenic volatile organic compounds (BVOC) are important atmospheric trace gases. They are involved in photochemical ozone- and particle formation and they impact

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reads:

$$\Phi = \Phi^S \cdot \frac{c_L \cdot \alpha \cdot \text{PAR}}{\sqrt{1 + \alpha^2 \cdot \text{PAR}^2}} \cdot \exp(\beta \cdot (T - T_S)) \quad (2)$$

In Eq. (2), Φ is the emission rate at temperature T and at light intensity PAR. Φ^S is the emission activity factor i.e. the emission rate measured at standard light intensity (often set to $1000 \mu\text{mol m}^{-2} \text{s}^{-1}$) and at standard temperature, T_S (often set to 30°C). α is the parameter describing the PAR dependence of the emission, and c_L is a normalization factor used to obtain $\Phi = \Phi^S$ when PAR is equal to the standard light intensity.

Equation (2) consists of three factors: first the emission activity factor, second the factor describing the PAR dependence and third the factor describing the temperature dependence. A factorial approach requires the individual factors to be independent of each other; i.e. Guenther et al. (1993) postulated that the PAR dependence is independent of the actual temperature and vice versa, that the temperature dependence is independent of the actual PAR.

Schuh et al. (1997) found interdependent impacts of temperature and PAR on MT emissions from sunflower which could not be described by a factorial approach as given in Eq. (2). They ascribed the observed interdependency to the two different mechanisms of MT emissions, MT emissions from pools that are independent of the actual light intensity and de-novo emissions that depend on the actual light intensity. Depending on the species, both mechanisms can act in parallel. Schuh et al. (1997) suggested two additive terms to describe T and PAR dependence of MT emissions. One of them was similar to Eq. (2) and was used to describe de-novo MT emissions. The other one was similar to Eq. (1) and describes the temperature dependence of MT emissions from pools. By using additive terms the factorial approach for de-novo emissions was retained.

In the same study, Schuh et al. (1997) noted the high variability of MT standard emission rates. Measuring emissions from different individuals of a given species under identical conditions of T and PAR still resulted in highly variable emission rates. This

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clearly shows that MT emissions also depend on other variables than T and PAR alone, and one of these other variables is soil moisture.

In the Model of Emissions of Gases and Aerosols from Nature (MEGAN, Guenther et al., 2006, 2012), impacts of soil moisture are only considered for isoprene emissions.

5 Guenther et al. (2006) implemented the empirical algorithm by Pegoraro et al. (2004) who used the volumetric water content, Θ , as reference quantity for characterizing the impacts of soil moisture. Three different regimes of Θ are used in MEGAN to define the factor that describes the impact of soil moisture on isoprene emissions. Above a threshold Θ_1 , isoprene emissions are not affected by soil moisture and the factor is unity. Below Θ_1 , isoprene emissions linearly decrease with decreasing Θ until the wilting point Θ_W is reached. The wilting point Θ_W is the soil moisture below which plants cannot extract water from the soil. At and below Θ_W isoprene emissions are set to zero. In MEGAN, Θ_W is taken from a database by Chen and Dudhia (2001). The difference: $\Theta_1 - \Theta_W$, $\Delta\Theta_1$, is the empirical parameter used to describe the dependence of isoprene emissions on soil moisture. Its value ($\Delta\Theta_1 = 0.06 \text{ m}^3 \text{ m}^{-3}$) is taken from Pegoraro et al. (2004).

Compared to isoprene there are less studies on impacts of soil moisture on MT emissions. Some studies show increasing emissions with decreasing soil moisture (Bertin and Staudt, 1996; Blanch et al., 2007; Ormeño et al., 2007), others show decreasing emissions with increasing severity of drought (Lavoit et al., 2009; Šimpraga et al., 2011). Besides this, different reference quantities have been used to characterize the soil moisture level. Among these are the plant water potential (Ormeño et al., 2007; Lavoit et al., 2009) and the diurnal variation of the radial stem diameter (Šimpraga et al., 2011). As these plant parameters are highly variable between individuals and influenced by a larger number of factors, they can hardly be used for up-scaling.

Aim of our study was thus to provide data that can be used for modelling the impacts of soil moisture on de-novo MT emissions. For this purpose we performed laboratory measurements with different plant species exposed to drought. We tested whether the volumetric water content Θ can be used as reference quantity and whether a factorial

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(Sartorius, MC1) that was used to measure the weight of the investigated plant together with the soil and the water in the soil. The flexibility of the bag that sealed the gap between stem and stem duct allowed weighing the plant/soil system on-line. The balance had a nominal resolution of 1 g but variations of the chamber's slight overpressure (5–10 mbar) imposed noise in the range of 20–30 g limiting the precision of weight measurements.

2.2 Determination of flux densities

Flux densities for the compound X , $\Phi(X)$, were calculated using the respective differences of the mixing ratios between chamber inlet and outlet and the leaf area, A_{leaf} , as basis:

$$\Phi(X) = \frac{F_{\text{air}} \cdot ([X]_i - [X])}{A_{\text{leaf}}} \quad (3)$$

In Eq. (3), F_{air} is the air flow through the chamber (in units of mol s^{-1}), $[X]_i$ is the mixing ratio of compound X at chamber inlet and $[X]$ is the mixing ratio of compound X in the chamber. Flux densities are termed as MT emission rates for $X = \text{MT}$, transpiration rates for $X = \text{H}_2\text{O}$, and net assimilation rates for $X = \text{CO}_2$. According to the results of several tests (e.g. Schuh et al., 1997; Heiden et al., 2003; Schimang et al., 2006) wall losses and chemical reactions were unimportant for all compounds investigated here and were therefore neglected. As a convention flux densities are positive when compounds are emitted (e.g. water, MT) and negative when compounds are taken up (e.g. CO_2). To allow better visual comparison in diagrams, net assimilation is multiplied by -1 .

Stomatal conductance was calculated using Eq. (4).

$$c(\text{H}_2\text{O}) = \frac{\phi(\text{H}_2\text{O})}{\Delta[\text{H}_2\text{O}]} \quad (4)$$

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CSTR. All plants were potted in the same soil that was a mix of peat (Einheitserde ED73 containing 2 g L^{-1} nutrient salts and 1 g L^{-1} clay) with quartz sand, volumetric ratio 5 : 1, density $0.46 \pm 0.07\text{ kg L}^{-1}$.

To control for the de-novo nature of the 1,8-cineol emission from the conifers we exposed the plants to $^{13}\text{CO}_2$. The chamber was flushed with synthetic air (Air Liquide, Germany) and $^{13}\text{CO}_2$ (99% ^{13}C , $\sim 350\text{ ppm}$) was added for $\sim 3\text{ h}$ in each of both experiments.

Individual plants were investigated for time periods of 3–10 weeks. In most of our studies, the impact of soil moisture was investigated (Table 1, European beech, two experiments with Holm oak – experiment Holm oak 1 and Holm oak 2 –, one experiment with Norway spruce and one with Scots pine). In these experiments the plants were exposed to a diurnal rhythm of 11 h illumination, 11 h darkness and simulation of twilight by switching on or off individual lamps within 1 h in the morning and evening, respectively.

In additional studies, we varied T or PAR, respectively, in parallel to soil moisture to investigate the potential limitations of the factorial approach. In the third experiment with Holm oak the chamber temperature was systematically changed during periods of illumination. Except for two days, the chamber temperature was set to 15°C during the night and kept at 15°C for the next 6–7 h of the following illumination period (from 3 o'clock to ~ 10 o'clock). Then the temperature was set to 20°C for four hours (from ~ 10 to ~ 14 o'clock) and thereafter to 25°C (from ~ 14 to ~ 18 o'clock, all data local time). The exact timing of temperature settings was adapted to the start of GC runs. The period of illumination was elongated to 15 h allowing measuring at the 3 different temperatures but at the same PAR for each day. When Θ had fallen below $0.02\text{ m}^3\text{ m}^{-3}$, the chamber temperature was not changed for two days to follow the drought induced decrease of MT emissions without changes of temperature and PAR.

In the fourth experiment with Holm oak, PAR was changed systematically during periods of illumination. Every second day PAR was set to $700\text{ }\mu\text{mol m}^{-2}\text{ s}^{-1}$ for 6 h (from 4 o'clock to ~ 10 o'clock), thereafter to $400\text{ }\mu\text{mol m}^{-2}\text{ s}^{-1}$ for 5 h (from ~ 10 to ~ 15

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with coefficients of determination always above $R^2 > 0.95$. The pattern was also not affected by the drought (Fig. 2) and therefore the effects of drought on de-novo MT emissions can be shown at the example of a single MT. For spruce and pine we choose 1,8-cineole emissions for the soil moisture dependence, because these were the only pure de-novo MT emissions from both conifers.

Sabinene was the dominant emission from European beech, comprising nearly 1/3 of the total emissions. Other MT emitted in substantial amounts were: γ -terpinene, α -terpinene, β -phellandrene, and α -terpinolene. We will show the response of European beech to drought at the example of sabinene. Main MT emissions from Holm oak were those of α -pinene, limonene, β -pinene, sabinene and myrcene. In two of the experiments with Holm oak α -pinene was the dominant emission (experiment 1: $\sim 48\%$ of total MT emissions; experiment 3: $\sim 42\%$ of total MT emissions), in the two other experiments the emissions of limonene were the strongest (experiment 2: limonene $\sim 45\%$, α -pinene $\sim 23\%$ of total MT emissions; experiment 4: limonene $\sim 39\%$, α -pinene $\sim 25\%$ of total MT emissions). To demonstrate the behaviour of MT emissions from Holm oak in response to drought we choose α -pinene as pivotal substance. It has to be noted that strong emissions of the acyclic ocimenes have been absent from Holm oaks. Emissions of ocimenes may show different behaviour than emissions of the cyclic MT (Staudt and Bertin, 1998). During our experiments the ocimene emissions were too low to significantly influence the sum of all MT emissions (maximum $\sim 6\%$ of total MT emissions).

3.2 Impacts of soil moisture

3.2.1 European beech

Figure 3 shows the time series of sabinene emissions from European beech over a period of about three weeks. According to the de-novo nature of the emissions a significant diurnal variation was observed with nearly no emissions during darkness and high emissions during periods of illumination. As can be seen in the Θ -trace, the plant

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was watered 4 times during the experiments. Between 2.5 and 5.6 L water were added after soil moisture had reached values of $\Theta \sim 0.1 \text{ m}^3 \text{ m}^{-3}$ (dry conditions) and Θ near to $0 \text{ m}^3 \text{ m}^{-3}$ (severe drought), respectively.

Besides the strong light dependent variation, also impacts of soil moisture on MT emissions were observable. During severe drought (2nd period, days 5–17 in Fig. 3) MT emissions decreased near to zero. After re-watering MT emissions increased again. Such increases were not instantaneous but appeared on a time scale of few days.

Transpiration (not shown in Fig. 3) and net assimilation showed similar responses to Θ as MT emissions but with different response times. As can be seen, changes in net assimilation appeared earlier than changes in MT emissions, in particular during the phase of the second drought period (Fig. 3, days 5–17).

Figure 4 shows the dependence of normalized sabinene emissions and net assimilation on Θ . Only data taken at $\text{PAR} = 440 \mu\text{mol m}^{-2} \text{ s}^{-1}$ are shown. For Θ between 0.35 and $0.1 \text{ m}^3 \text{ m}^{-3}$, MT emissions showed a considerable scatter that was mainly caused by different response times for the emissions to increase to pre-drought levels. With Θ falling below $0.1 \text{ m}^3 \text{ m}^{-3}$ emissions decreased to minute amounts. As obvious from Fig. 4, changes of net assimilation as response to decreasing soil moisture were different from those of MT emissions. Net assimilation already decreased at higher Θ of $\sim 0.22 \text{ m}^3 \text{ m}^{-3}$.

3.2.2 Holm oak

Two experiments with Holm oak were set up to investigate whether the reduction of MT emissions with decreasing Θ was determined by the soil moisture or by some other time constant of the plant itself (Table 1, experiment Holm oak 1 and Holm oak 2). Holm oak 1 was investigated at higher PAR and at higher T and showed higher rates of net photosynthesis and higher transpiration (data not shown). The soil and the plants roots were also exposed to higher temperature compared to Holm oak 2. Due to the combination of higher evaporation and transpiration rates, Θ dropped from

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$\sim 0.1 \text{ m}^3 \text{ m}^{-3}$ to $\sim 0.03 \text{ m}^3 \text{ m}^{-3}$ within 8 days, faster than for Holm oak 2 where it took about 18 days.

The MT emissions decreased also on different time scales in the two experiments (see Fig. 5a). In contrast, the decrease of MT emissions with decreasing Θ was similar for both individuals although they were investigated at different dynamics of drought progression (Fig. 5b). The substantial difference observed for the temporal behaviour of the emissions (Fig. 5a) did not cause significant changes in decrease of emission rates for $\Theta < 0.1 \text{ m}^3 \text{ m}^{-3}$ (Fig. 5b). Similar as for beech, increasing MT emissions were observed for Holm oak when Θ declined from $\sim 0.4 \text{ m}^3 \text{ m}^{-3}$ to $0.15 \text{ m}^3 \text{ m}^{-3}$. For Holm oak 1, at higher T and PAR, the emissions increased nearly 3-fold. For Holm oak 2 the increase was about 40 %.

In the third experiment with Holm oak chamber temperature was changed systematically during the progressing drought (Table 1, experiment Holm oak 3). This experiment was designed to measure the impact of Θ on MT emissions at different temperatures as well as the temperature dependence at different stages of drought.

The temperature dependence of MT emissions was determined by linear regression analysis of $\ln(\Phi)$ vs. leaf temperatures (see Eqs. 1 or 2 third factor). During the first 9 days with varying temperature at $\Theta > 0.1 \text{ m}^3 \text{ m}^{-3}$ the temperature dependence remained constant with $\beta = 0.12 \pm 0.007 \text{ K}^{-1}$ (mean, 1σ standard deviation).

Similar to the observations in the other experiments with Holm oak, MT emissions decreased when Θ fell below $0.06 \text{ m}^3 \text{ m}^{-3}$. During this measurement period the impacts of progressing drought and variations of temperature superimposed each other. Although temperature increased systematically over the day, emissions did not increase substantially. Consistent with the findings reported by Bertin and Staudt (1996), typical log-linear relationships between emissions and temperature were hardly detected. We therefore had to correct the data to consider the drought induced decrease of MT emissions over the day.

Approaches to determine the Θ dependence from the data obtained at the days when temperature was held constant were not successful. The small dynamic range in

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temperature. The emission rates measured the next day under conditions of variable PAR were then corrected by dividing them by the correction factors. After correction the data were normalized using the emission rates measured at the respective day at PAR = 700 $\mu\text{mol m}^{-2} \text{s}^{-1}$. Figure 7 shows the normalised emission as a function of light intensity at the example of 3 days. Within the precision of the data the light intensity dependence did not substantially or systematically change with progressing drought.

3.2.3 Scots pine and Norway spruce

The experiments with pine and spruce lasted for about a month each and each of the plants was exposed to 3 drought periods. At least one of these drought applications was severe with $\Theta < 0.01 \text{ m}^3 \text{ m}^{-3}$.

Main emissions from both conifers were pool MT emissions such as α -pinene and Δ -3-carene. Besides such pool emissions the plants also emitted 1,8-cineole which is a de-novo emission (Tarvainen et al., 2005; Kleist et al., 2012). This was also tested for both individuals used in our experiments by exposing them to $^{13}\text{CO}_2$. After three hours of $^{13}\text{CO}_2$ exposure 1,8-cineole was strongly labeled indicating that 1,8-cineole was a de-novo emission with negligible contribution of pool emissions. We here focus on the Θ dependence of 1,8-cineole in order to compare with results obtained for the de-novo MT emissions from the deciduous species.

Emissions of 1,8-cineole from both species behaved similar to the de-novo MT emissions from the broadleaf species. When Θ dropped from $0.35 \text{ m}^3 \text{ m}^{-3}$ to the respective thresholds Θ_1 the emissions slightly increased ($\sim 30\%$ for spruce and $\sim 50\%$ for pine). Below Θ_1 the 1,8-cineole emissions decreased and approached nearly zero. After re-watering, MT emissions recovered on a time scale of days and reached levels similar to those before the drought. All in all, the de-novo emissions of pine and spruce behaved the same as the de-novo MT emissions from the broadleaf species. Data of dependency of the 1,8-cineole emissions on Θ are listed in Table 2 together with the data obtained in the other experiments.

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plying $\beta \sim 0.12 \text{ K}^{-1}$, the main fraction of increases in MT emissions from these plants was explained by the increase of leaf temperature. Only for one single Holm oak we found an increase (\sim three fold, see Fig. 5b, red circles) too high to be explained by increases in leaf temperature alone.

Due to the watering-drought-watering procedure used here it is possible that parts of the increases arise from recovery from a preceding drought. In particular when Θ decreases rapidly, the effects of sequential droughts may overlap. However, the effect of strongly increasing MT emissions with Θ dropping from high levels to Θ_1 was observed in one experiment only and without further information we can only speculate on this effect.

The reason for increases of the 1,8-cineole emissions from conifers during mild drought stress ($\sim 30\text{--}50\%$ when Θ dropped from 0.35 to $0.1 \text{ m}^3 \text{ m}^{-3}$) also remains unproven because leaf temperatures were not reliably measurable for both conifers. Nevertheless it is reasonable to assume that also in conifer species needle temperature increase due to lower transpirational cooling caused the observed slight increases in MT emissions.

For modelling of isoprene emissions in MEGAN, the impact of leaf temperature is implemented by a general temperature dependence of the emissions. Such parameterization cannot differentiate between variations of leaf temperature by variations in transpiration or by variations of air temperature. Therefore the indirect effect of drought does not appear in the factor for the dependence of isoprene emissions on soil moisture (Guenther et al., 2006). In analogy we suggest, to consider decreasing emissions caused by severe drought stress also for de-novo MT emissions.

4.1.2 Severe drought stress

Similar to previous studies (e.g. Bertin and Staudt, 1996; Llusia and Peñuelas, 1998; Plaza et al., 2005; Lavoit et al., 2009; Šimpraga et al., 2011; Bourtsoukidis et al., 2014) we observed substantially reduced MT emissions during periods of severe drought

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an empirical relationship between de-novo MT emissions and Θ . Nevertheless, when reflecting mechanisms of the drought impact, plant physiological processes must be considered. For isoprene the decreasing emissions as result of drought are ascribed to a general decrease of the plant's performance (e.g. Brüggemann and Schnitzler, 2002). Decreased plant performance causes reduction of isoprene biosynthesis and thus isoprene emissions. Basic parts of isoprene and MT biosynthesis pathways are identical suggesting that general mechanisms causing the reduction of isoprene and MT emissions are similar. We therefore suggest that, similar to isoprene emissions, also the decrease of de-novo MT emissions is caused by a general decrease of the plants performance.

As plant performance is coupled to the rate of transpiration and to net assimilation either of them may be regarded as reference quantity. But, as already pointed out by Peñuelas et al. (2009) and by Loreto and Schnitzler (2010), drought induced responses in transpiration or net assimilation differ from responses in MT emissions. This general behavior was also found here in all experiments and we therefore could not use either of them as reference quantity.

We used Θ as reference, but, from a mechanistic point of view Θ is not a direct reference quantity. In a first step, soil moisture impacts the plants performance and in a second step the plants performance affects MT synthesis and emissions. The relationship found here between de-novo MT emissions and Θ therefore has to be scrutinized. In particular the temporal behaviour of MT emissions may be skewed by the time needed for the plant to respond to changes in Θ .

Indeed there were time periods with substantial time lags between changes of Θ and the plants responses in MT emissions. Re-watering caused Θ to increase to optimum conditions for the plants on time scales of hours. For the de-novo MT emissions it took some days until the same level was reached as before the drought. We assume that the time needed for the plants to recover from previous droughts was the reason for the decoupling of Θ and MT emissions during such time periods.

Quick changes of Θ also appear in nature in case of strong rainfall. If such rainfall appears after a severe drought period with Θ being far below the threshold affecting emissions, Θ and emissions are most probably also decoupled in nature impeding a correct description of the emission temporal behavior during such periods.

We tested whether or not a mechanistic model can be used to describe the impacts of soil moisture on MT emissions. Niinemets et al. (2002) couple de-novo MT emissions to photosynthetic electron transport. Using the fraction of the photosynthetic electron transport necessary for MT synthesis (ε) as a surrogate for standard emissions shall lead to a more realistic description of emissions, especially under stress conditions where empiric models are supposed to fail (Niinemets et al., 2002).

For our tests we used the data from beech during a period of mild drought and re-watering when stomatal conductance was still reliably measurable to test the model (Fig. 3, days 0 to 11). ε was calculated as described in Niinemets et al. (2002) and plotted as a function of Θ (Fig. 8).

There was no significant change in ε when Θ changed rapidly due to re-watering, indicating that a coupling of MT emissions to the fraction of electron transport may be usable for describing periods of recovery. However, ε was not constant when Θ was between $0.2 \text{ m}^3 \text{ m}^{-3}$ and $0.1 \text{ m}^3 \text{ m}^{-3}$. This may be caused by the mild drought itself or by the changes in leaf temperature. However, impacts of soil moisture on MT emissions during desiccation cannot be described using a constant value for ε . Empirical parameterizations have to be included also in this model to allow realistic description of BVOC emissions (Arneeth et al., 2007).

We tried to derive such empirical relationship to allow describing ε in dependence of soil moisture but these attempts were unsuccessful. With progressing drought MT emissions were still strong although transpiration and net assimilation were already very low. ε is related to leaf internal CO_2 concentration which is coupled to stomatal conductance. Reliable calculations of stomatal conductance require reliable data on transpiration but our data on stomatal conductance at such low transpiration were error prone. We therefore cannot provide reliable data for ε at $\Theta \leq 0.1 \text{ m}^3 \text{ m}^{-3}$.

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While phenomenological derived algorithms cannot describe the emissions during recovery after severe drought, they can describe impacts of soil moisture during desiccation. Desiccation appears on longer time scales than changes of soil moisture after heavy rain fall. For such longer time scales, the lag between changes of Θ and the plants' response should not carry too much weight in skewing the relationship between emissions and Θ . This assumption was confirmed by the result from the two experiments with Holm oak at different temporal progression of drought. Although the temporal decreases appeared on different time scales the Θ dependence of MT emissions remained similar (compare Fig. 5a and b). As long as desiccation appeared on a time scale of days, the plant responses to changes in Θ were obviously quick enough to allow finding the relationship between Θ and de-novo MT emissions. Although Θ is only an indirect reference quantity for plant performance, it proved to be suitable for considering the impacts of soil moisture on de-novo MT emissions in modelling.

4.4 Justification of a multiplicative approach for modelling

Modelling BVOC emissions is often performed using factorial approaches. An important requirement for the validity of such a factorial approach is a negligible interdependency of the individual factors. We investigated such possible interdependencies but no substantial effects were found.

As can be seen from Fig. 6, the temperature dependence of MT emissions from Holm oak was largely independent of the actual Θ . Vice versa, the soil moisture dependence of the emissions was independent of the actual temperature (compare data in Table 2). Also the PAR dependence of MT emissions from this species was not substantially affected by the actual soil moisture (Fig. 7) and vice versa the Θ dependence was not substantially influenced by PAR (Table 2). Compared to the overall effect of drought on de-novo MT emissions, possible residual interdependencies were negligible. This indicates that a factorial approach is justified at least for Holm oak investigated with this respect. From the similarity of basic processes leading to de-novo MT emissions we postulate that such interdependencies are also negligible for other plant species.

5 Conclusions

All de-novo MT emissions from all plants investigated in our experiments clearly depended on soil moisture. The investigated species are representative for European climate zones and they all are strong MT emitters. We therefore conclude that impacts of drought have to be re-considered for modelling.

To the best of our knowledge the direct impacts of soil moisture on constitutive de-novo MT emissions are not considered in MEGAN. Severe drought reduces the emissions and therefore models neglecting impacts of soil moisture overestimate MT emissions. Depending on the climatology in the respective regions and depending on the fraction of de-novo emitted MT, modelled MT emissions may drop substantially when considering soil moisture as variable influencing de-novo MT emissions.

On the other hand to the best of our knowledge a dependence of the fraction of the photosynthetic electron transport necessary for MT synthesis, ε , on soil moisture is not considered in modelling so far. According to our data ε increased already two-fold when Θ dropped to $\sim 0.2 \text{ m}^3 \text{ m}^{-3}$. Hence, simulations of de-novo MT emissions assuming ε to be constant will underestimate their source strengths at conditions of moderate drought. Again, depending on the climatology of the respective regions and the fraction of de-novo emitters in the respective region, modelled de-novo MT emissions may increase substantially. Large differences of modelling results for MT emissions (Arneeth et al., 2008) may therefore be reduced to some extent.

Although the detailed mechanisms causing the reductions in de-novo MT emissions are still unknown, one statement can be made. Estimations of future alterations of MT emissions must consider such effects because climate change will induce more and longer lasting drought periods (Dai, 2013). Future long lasting drought periods will suppress constitutive de-novo MT emissions. In combination with more intensive heat periods that also suppress de-novo MT emissions (Kleist et al., 2012), these abiotic stresses will have substantial impacts on regional and global BVOC emissions.

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Table 1. List of experiments and chamber settings.

| Plant | Purpose of experiment | Leaf area [m ²] | Chamber temperature [°C] | PAR [μmol m ⁻² s ⁻¹] |
|----------------|-----------------------------|-----------------------------|--------------------------|---|
| European beech | Θ-dependence | 0.91 | 23 | 440 |
| Holm oak 1 | Θ-dependence | 0.25 | 25 | 600 |
| Holm oak 2 | Θ-dependence | 0.27 | 22 | 440 |
| Norway spruce | Θ-dependence | 0.7 | 23 | 440 |
| Scots pine | Θ-dependence | 0.45 | 25 | 400 |
| Holm oak 3 | Θ- and <i>T</i> -dependence | 0.18 | 15 | 500 |
| Holm oak 3 | Θ- and <i>T</i> -dependence | | 20 | 500 |
| Holm oak 3 | Θ- and <i>T</i> -dependence | | 25 | 500 |
| Holm oak 4 | Θ- and PAR-dependence | 0.25 | 20 | 700 |
| Holm oak 4 | Θ- and PAR-dependence | | 20 | 400 |
| Holm oak 4 | Θ- and PAR-dependence | | 20 | 200 |

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Table 2. Data from fits of emission rates vs. Θ . EB = European beech, HO = Holm oak, NS = Norway spruce, SP = Scots pine. Numbers behind species indicate experiment number according to the succession of the experiments described in Sect. 3. Data behind the slash give chamber temperatures in $^{\circ}\text{C}$ and PAR in $\mu\text{mol m}^{-2} \text{s}^{-1}$, respectively. Φ^{th} (MT) and Φ^{th} (ΣMT) are the emission rates measured for the MT listed in the second column and for the sum of all MT emissions, respectively as measured near to Θ_1 . Θ_1 is the volumetric water content of the soil when emissions start to decrease ($\Theta_1 = \Delta\Theta_1 + \Theta_0$). Θ_0 = intercept of linear regression analysis when MT emissions are extrapolated to be zero. $\Delta\Theta_1$ is the range of Θ in which the emissions drop from their maximum to zero.

| | MT | Φ^{th} (MT) [$\text{nmol m}^{-2} \text{s}^{-1}$] | Φ^{th} (ΣMT) [$\text{nmol m}^{-2} \text{s}^{-1}$] | $\Delta\Theta_1$ $\text{m}^3 \text{m}^{-3}$ | Θ_0 $\text{m}^3 \text{m}^{-3}$ |
|---------|------------------|---|--|--|--|
| EB | Sabinene | 0.9 ± 0.03 | 2.6 ± 0.04 | 0.09 ± 0.004 | 0.03 ± 0.002 |
| HO1 | α -pinene | 4.9 ± 0.45 | 10.2 ± 0.47 | 0.044 ± 0.004 | 0.058 ± 0.002 |
| HO2 | α -pinene | 2.1 ± 0.05 | 9.2 ± 0.25 | 0.063 ± 0.003 | 0.071 ± 0.002 |
| NS | 1,8-cin. | $(3.3 \pm 1.1) \times 10^{-4}$ | | 0.19 ± 0.01 | 0.02 ± 0.007 |
| SP | 1,8-cin. | 0.88 ± 0.15 | | 0.068 ± 0.005 | 0.041 ± 0.004 |
| HO3/15 | α -pinene | 3.5 ± 0.08 | 7.9 ± 0.74 | 0.055 ± 0.01 | -0.006 ± 0.007 |
| HO3/20 | α -pinene | 4.8 ± 0.22 | 11.7 ± 0.6 | 0.058 ± 0.008 | -0.01 ± 0.004 |
| HO3/25 | α -pinene | 6.5 ± 0.34 | 15.9 ± 0.8 | 0.079 ± 0.016 | -0.021 ± 0.008 |
| HO4/700 | α -pinene | 1.6 ± 0.18 | 6.7 ± 0.8 | 0.065 ± 0.008 | 0.016 ± 0.006 |
| HO4/400 | α -pinene | 0.7 ± 0.1 | 2.6 ± 0.4 | 0.045 ± 0.015 | 0.018 ± 0.012 |
| HO4/200 | α -pinene | 0.3 ± 0.04 | 1.2 ± 0.17 | 0.044 ± 0.015 | 0.019 ± 0.012 |

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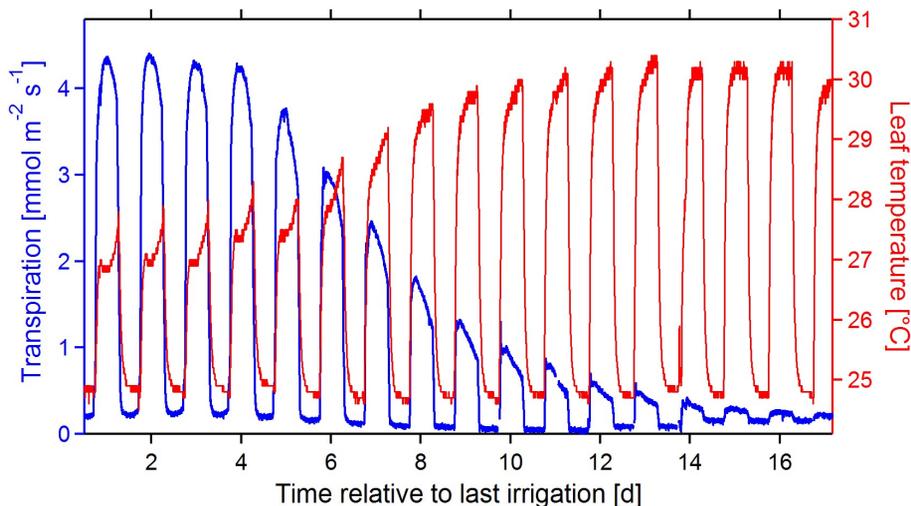


Figure 1. Temporal development of transpiration (blue trace left handy-axis) and leaf temperature (red trace, right hand y-axis, average of three leaves) at the example of Holm oak, experiment 1. The plant was irrigated at day 0 ($\Theta = 0.4 \text{ m}^3 \text{ m}^{-3}$). At the end of the drought period Θ had fallen to $0.05 \text{ m}^3 \text{ m}^{-3}$. Chamber temperature 25°C , PAR = $600 \mu\text{mol m}^{-2} \text{ s}^{-1}$.

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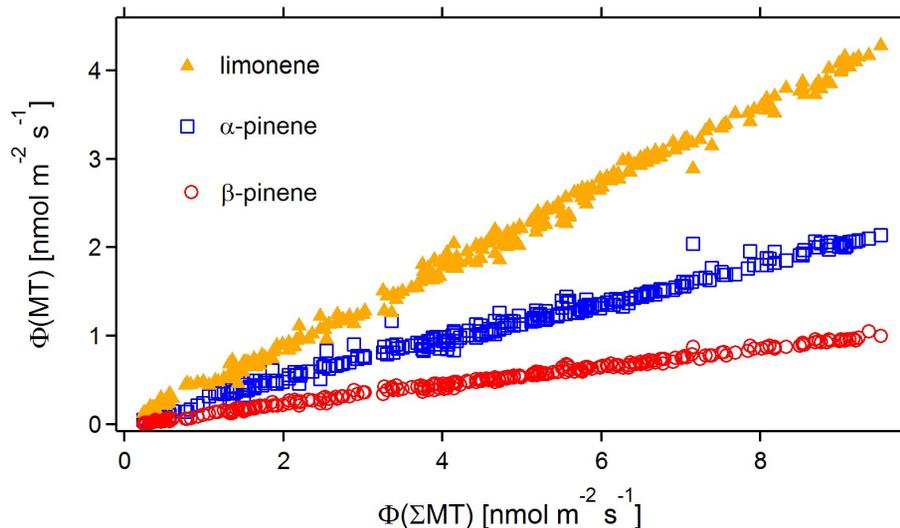


Figure 2. Correlation plot of emission rates measured for Holm oak, experiment 2. Only data measured at a PAR of $440 \mu\text{mol m}^{-2} \text{s}^{-1}$ and a chamber temperature of 22°C are plotted. The variation of emission rates is caused by changes in soil moisture. The high coefficients of determination ($R^2 > 0.95$) indicate that only the strengths of the emissions was changed but not the emission pattern.

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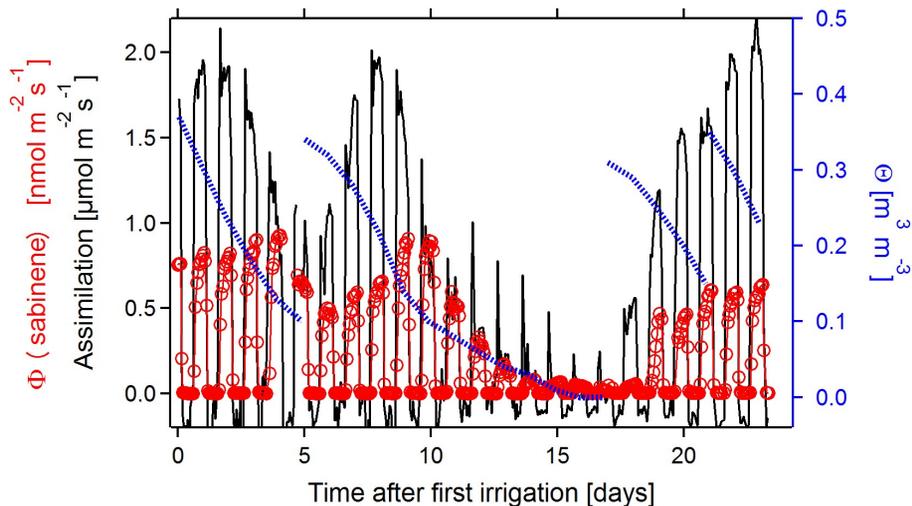


Figure 3. Long term time series of sabinene emissions from a European beech seedling (red circles, left hand y-scale), assimilation (multiplied by -1 , black line, left hand y-scale) and volumetric water content of the soil Θ (blue dashed line, right hand y-scale).

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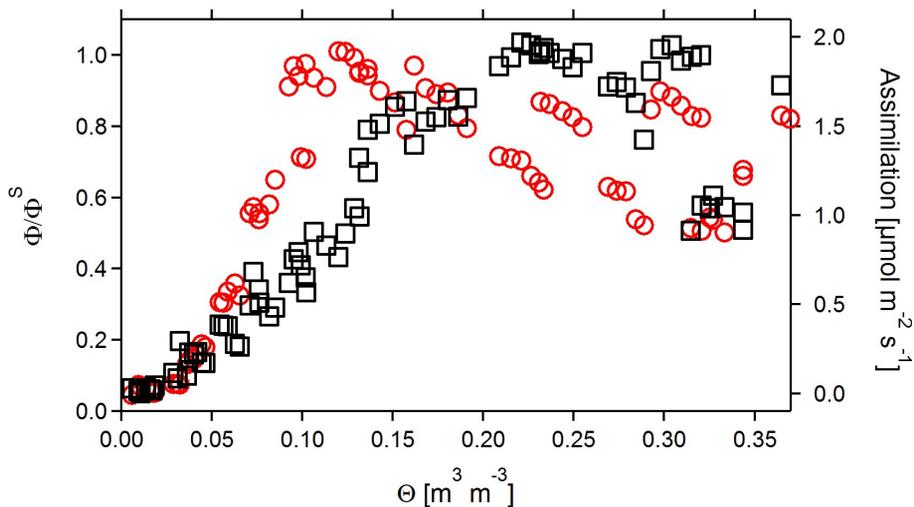


Figure 4. Normalised sabinene emissions from beech (red circles, left scale) and rates of net photosynthesis (black squares, right scale, multiplied by -1) in dependence on Θ . Only data taken at a chamber temperature of 23°C and a PAR of $440\ \mu\text{mol m}^{-2}\ \text{s}^{-1}$ are considered.

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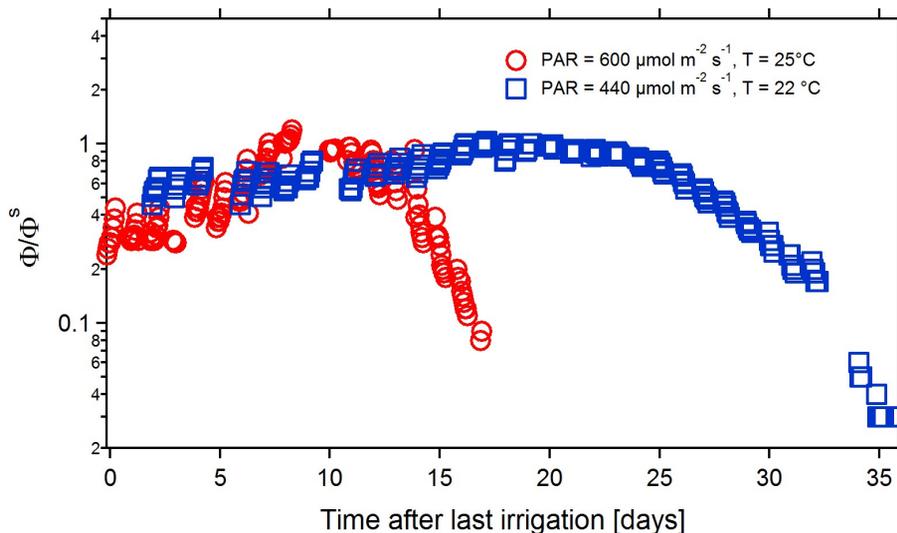


Figure 5a. Temporal shape of normalised α -pinene emissions from two individuals of Holm oak, experiments Holm oak 1 and Holm oak 2. Red circles show the data obtained at higher PAR and at higher chamber temperature. Blue squares show the data obtained for the plant investigated at lower temperature and PAR. Only data taken during periods of full illumination are shown. For better comparison the emissions were separately normalized to the emission rates measured for the respective individual at $\Theta \sim 0.12 \text{ m}^3 \text{ m}^{-3}$.

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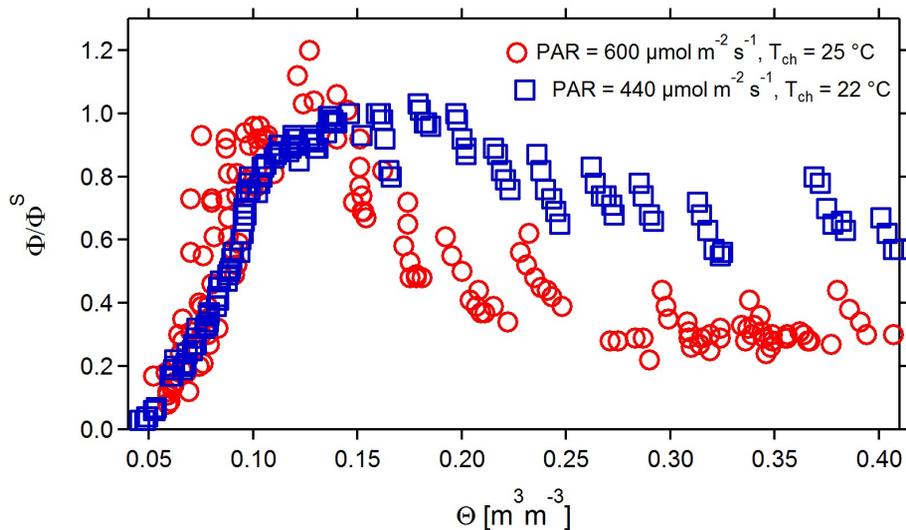


Figure 5b. Normalized α -pinene emissions from Holm oak in dependence of Θ . Red circles show the data measured for the plant investigated at higher PAR and higher chamber temperature, blue squares show data taken for the plant investigated at lower PAR and lower temperature. Same data as in Fig. 5a.

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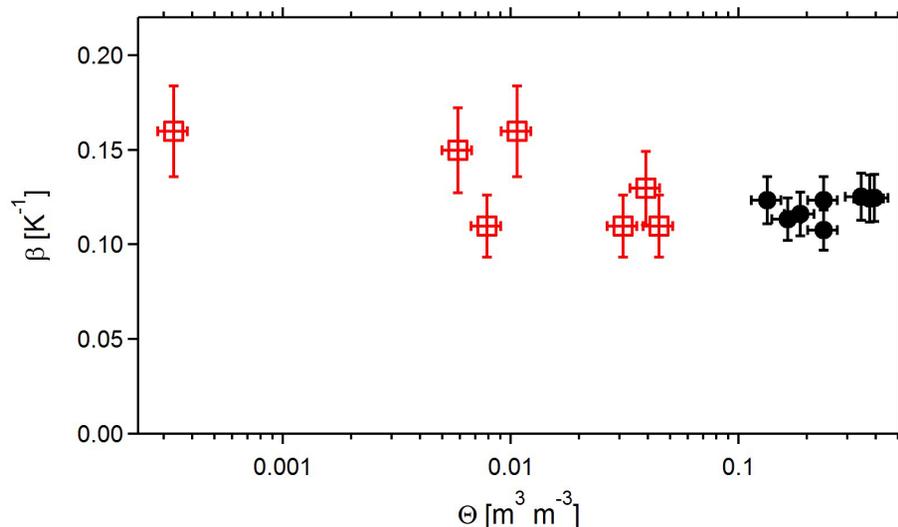


Figure 6. Temperature coefficient β for α -pinene emissions from Holm oak (experiment 3) at different soil moisture. Closed black circles represent the data obtained without impacts of drought on MT emissions. Red squares represent the data obtained for $\Theta < 0.06 \text{ m}^3 \text{ m}^{-3}$ after correcting for the drought induced decrease of emissions. Errors in β were about $\pm 0.01 \text{ K}^{-1}$ for the data obtained without drought stress. For the data obtained during drought stress the errors from the normalization procedure had to be taken into account and errors in β are estimated to $\pm 0.03 \text{ K}^{-1}$. Error in Θ is estimated to $\pm 15\%$. For better visualization of data at low Θ , logarithmic x-axis was used.

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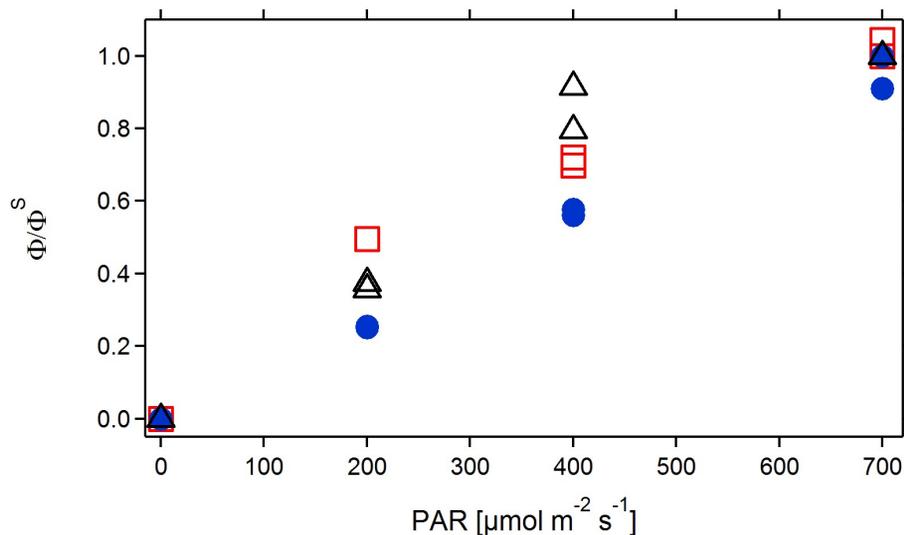


Figure 7. Emission rates corrected for the temporal decrease due to the progressing drought and normalized to the emission rates measured the respective day at $\text{PAR} = 700 \mu\text{mol m}^{-2} \text{s}^{-1}$ as function of PAR. Blue circles represent data taken at $\Theta \sim 0.055 \text{ m}^3 \text{m}^{-3}$, black triangles show data taken at $\Theta \sim 0.043 \text{ m}^3 \text{m}^{-3}$ and red squares show the data obtained at $\Theta \sim 0.018 \text{ m}^3 \text{m}^{-3}$. Experiment Holm oak 4, absolute emission rates measured at $700 \mu\text{mol m}^{-2} \text{s}^{-1}$ dropped by a factor of about 40 with Θ falling from $0.055 \text{ m}^3 \text{m}^{-3}$ to $0.018 \text{ m}^3 \text{m}^{-3}$.

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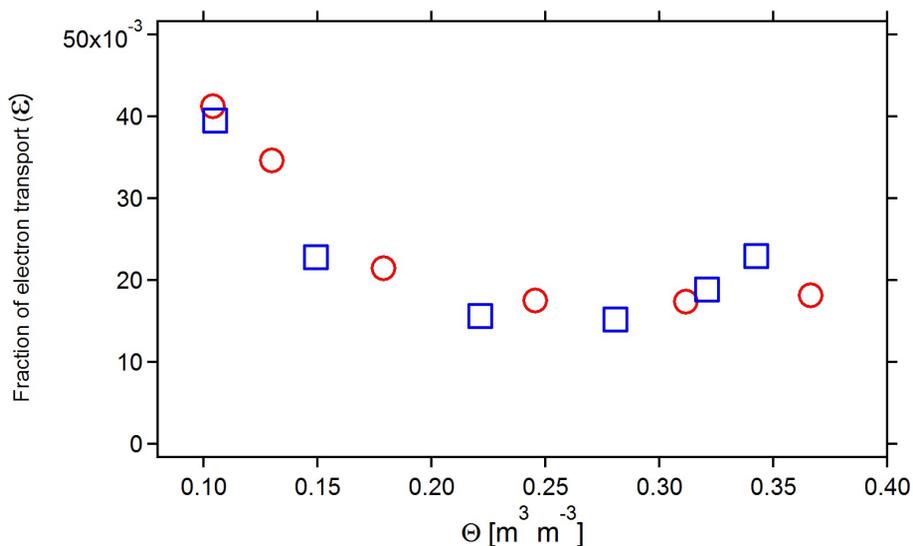


Figure 8. Fraction of photosynthetic electron transport used for MT synthesis, ϵ , calculated according to Niinemets et al. (2002) in dependence of Θ . The data were calculated as daily averages. Red circles represent ϵ as determined for the first measurement period during mild drought (Fig. 3, days 0–5) when Θ dropped to $\sim 0.1 \text{ m}^3 \text{ m}^{-3}$. Blue squares show the data after re-watering at day 6 until day 11 when Θ again had dropped to $\sim 0.1 \text{ m}^3 \text{ m}^{-3}$. Experiment with European beech.

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