

Effect of drought on isoprene emission rates from leaves of *Quercus virginiana* Mill.

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Abstract

Leaf isoprene emission rates (F_{iso}) were studied in 2-year old trees of live oak (*Quercus virginiana* Mill.) during two drying–rewatering cycles. During the first drying–rewatering cycle, photosynthesis (A) and stomatal conductance (g_s) decreased by 92% ($\pm 7\%$) and 91% ($\pm 8\%$), respectively, while F_{iso} remained essentially constant for 8 days of treatment. After 12 days under severe drought conditions, F_{iso} was reduced by 64% ($\pm 6\%$). Similar values were found during the second drying–rewatering cycle. During the recovery phase of both cycles, F_{iso} recovered more quickly than A and g_s . The lower drought sensitivity of F_{iso} compared with that of A resulted in a higher percentage of fixed C lost as isoprene (C_{iso}/C_A) as plants became more stressed, reaching peaks of 50% when A was almost zero. F_{iso} showed a strong negative linear relationship with pre-dawn leaf water potential (ψ_{PD}) that could be a useful parameter to include in isoprene emission models to account for effects of drought stress on leaf F_{iso} .

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1. Introduction

Isoprene is the most abundant hydrocarbon emitted by many tree species with an annual global flux estimated at 5×10^{14} g year⁻¹ (Guenther et al., 1995). Because of its high reactivity, isoprene exerts profound

effects on tropospheric chemistry through the production of ozone and other oxidants, and increases the lifetime of greenhouse gases such as methane. For this reason, there is an increasing need to understand the effect of future climate change scenarios on isoprene production.

Several environmental factors are known to affect the emission of isoprene by plants (Harley et al., 1999; Fuentes et al., 2000). Some studies have focused on the effect of water-stress on isoprene emission rates (F_{iso}) (e.g. Tingey et al., 1981; Sharkey and Loreto, 1993; Lerdau et al., 1997; Guenther et al., 1999; Bruggemann and Schnitzler, 2002). Although in general F_{iso} were much less sensitive to drought than photosynthetic rates (A), results are variable among studies and no clear

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pattern has been observed. Some studies have observed that plants can exhibit higher F_{iso} upon relief of water-stress than in pre-stress conditions (Sharkey and Loreto, 1993).

It is known that isoprene biosynthesis occurs within the chloroplast, and early experiments with isotopically labelled carbon dioxide ($^{13}\text{CO}_2$) have shown that ca. 80% of the C in isoprene is derived from newly assimilated photosynthetic C (Sanadze et al., 1972; Mgaloblishvili et al., 1979), with roughly 20% coming from alternate sources (Karl et al., 2002; Schnitzler et al., 2004). A recent study showed that under stress conditions such as water-stress or high-temperature, this partitioning may vary in favour of alternate sources under conditions of low A (Funk et al., 2004). Typically, in non-stressed conditions, the percentage of assimilated C emitted as isoprene (C_{iso}/C_A) at 30 °C is around 2%, which represents a non-trivial loss of C to the plant (Sharkey et al., 1991; Baldocchi et al., 1995; Monson and Fall, 1989; Harley et al., 1999; Fang et al., 1996). However, the C loss can exceed 50% during periods of stress when A is depressed (Sharkey and Loreto, 1993).

In order to improve our understanding of the environmental and physiological control on F_{iso} from temperate tree species, we conducted a controlled laboratory experiment. The specific objectives of the study were: (1) to investigate the effect of water-stress on F_{iso} , specifically the short (days) and medium-term (weeks) response of F_{iso} to drought stress; (2) to explore the relationship between F_{iso} and A ; (3) to calculate the isoprene: carbon dioxide flux ratio for this species, under normal and water-stress conditions; (4) to find a physiological parameter that could be used in models to estimate the F_{iso} response to water-stress. It was hypothesised that: (a) in the short-term (few days), the F_{iso} are less sensitive to water-stress than A ; (b) in the medium-term, the F_{iso} will correlate with a physiological parameter of stress.

2. Materials and methods

2.1. Plant material

In January 2002, 16 2-year old trees of Live oak (*Quercus virginiana* Mill.) were obtained from the Camellia Forest Nursery (Chapel Hill, NC, USA). The 2-year old trees were transplanted to 6 dm³ plastic pots (30 cm high and 16 cm wide) containing commercial potting soil (Miracle Grow) and placed in the National Center for Atmospheric Research (NCAR, Boulder, CO) phytotron (a temperature-controlled greenhouse with supplemental lighting) for 70 days until the end of March when the experiment started.

2.2. Experimental design

Eight of the trees in the phytotron were randomly chosen as 'control' plants (C) (well-watered plants) and eight as 'treatment' plants (T) (subject to drought stress). Four of these plants (two treatment and two control) were used for destructive sampling and were monitored continuously for leaf temperature (T_{leaf}) and soil volumetric water content (θ) with leaf thermocouples (0.1 mm in diameter) and Delta-T probes (ML2 Theta Probe, Delta-T Devices, Cambridge, UK), respectively, connected to a datalogger (CR10, Campbell Scientific, Logan, UT, USA). These plants were not used for the F_{iso} measurements. In order to take into account the influence of growing conditions inside the phytotron on F_{iso} , air temperature (T_{air}), relative humidity (RH), and photosynthetic active radiation (PAR) were continuously measured and stored on an hourly basis in a CR10 datalogger.

Water-stress was imposed on eight previously non-stressed plants by withholding water during two successive drying–rewatering cycles. In the first cycle water was withheld from 21 March to 2 April (12 days) and in the second cycle from 18 April to 28 April (10 days). During both cycles, T plants were watered to field capacity approximately 12 h before the start of the drought phase of each cycle. Initially, A and F_{iso} were measured every three days and then daily when F_{iso} started to change more dramatically after treatment. The drying cycle was ended when F_{iso} of the T plants were reduced to less than 50% of the values measured in the C plants. At the end of each drought period, T plants were watered daily over the following recovery period (the first from 2 April to 18 April, the second from 28 April to 8 May) to allow plants to recover before starting the following cycle. The end of the recovery period in the first cycle was established as the time when the F_{iso} measured in the T plants reached the same mean emission rates as those measured in the C plants. During the first cycle, C plants were watered every 3 days, whereas during the second cycle they were watered every other day. The watering regime was changed to every other day because during the first cycle the C plants suffered a slight water-stress that affected mainly A and g_s .

2.3. Water status

In order to monitor water-stress the following parameters were measured: θ , pot mass (M) and pre-dawn leaf water potential (ψ_{PD}). θ was continuously monitored over the duration of the entire experiment using two Delta-T soil moisture sensors. The two sensors were inserted to 10 cm depth into the pot of a T plant and a C plant, and hourly average signals were collected with a CR10 data logger. In addition, θ was

measured with a portable sensor (ML2x Theta Probe, Delta-T Devices, Cambridge, UK), inserted into the pot at the time of each gas exchange measurement. M and θ were measured at the time of each gas exchange measurement just before putting the leaf into the leaf cuvette.

ψ_{PD} was measured using detached leaves with a Scholander pressure chamber (Model 610 Pressure Chamber, PMS Instrument Co., Corvallis, OR, USA). Because measurements with the pressure bomb are destructive, leaves used for these measurements were collected from the two T and two C plants that were not used for F_{iso} measurements. However, during the drying period of the second cycle ψ_{PD} was also measured in leaves from the 12 T and C plants to increase the number of replicates.

2.4. Sampling protocol

All gas exchanges, θ , pot mass, and ψ_{PD} measurements were performed in a single day using one leaf per plant for the gas exchange measurements. Two different leaves on each plant were used for measurements in the two cycles. At the beginning of the experiment, fully expanded leaves from the top of the canopy were randomly chosen and tagged for subsequent measurements. Prior to measurement, each plant was taken from the greenhouse to an adjacent laboratory where a gas exchange measurement system was set up. After a 15 min period at a PAR of $600 \mu\text{mol m}^{-2} \text{s}^{-1}$, the gas exchange measurements were started.

2.5. Leaf gas exchange measurements

A , g_s and intercellular CO_2 concentration (C_i) were measured using a LI-6400 gas exchange measurement system (Li-Cor, Lincoln, NE, USA). To avoid large oscillations in the CO_2 level of the air supply ($374 \mu\text{mol mol}^{-1} \pm 4\%$), the LI-6400 inlet drew air from outside the laboratory and an empty canister of 2 dm^3 volume was placed in line before the instrument to buffer against short-term variations. The air supply was humidified using an in-line bubbler because of the very low RH of the external air. RH inside the cuvette was maintained at $60\% (\pm 10\%)$.

For measurements of F_{iso} , an air sample of 300 ml was pulled from the outlet of the leaf cuvette through a 'T' junction and 20 cm of Teflon[®] PFA tubing into a custom-made inlet system capable of vacuum sample collection and isoprene cryofocusing. The isoprene sample was then transferred to the 0.25 mm ID \times 30 m MXT-624 capillary column (RESTEK Corporation, Bellefonte, PA, USA) of a portable gas chromatograph (SRI 310, Buck Scientific, East Norwalk, CT, USA) by a flow of high-purity He that was used as carrier gas. Isoprene was separated with a carrier (He) flow of

3 ml min^{-1} and with a temperature programme from 40 to 200°C at $10^\circ\text{C min}^{-1}$. Isoprene eluting from the column was measured using a flame ionisation detector (FID), and the peak was integrated using PeakSimple-32 integrator (SRI, Buck Scientific, East Norwalk, CT, USA). Additional details of the analytical system can be found in Greenberg et al. (2003). Before the start of the experiment the FID-gas chromatograph was tested for a few days for linear response and detection stability. The linearity and the good stability (ca. 2%) of the results suggested that a single injection of a known isoprene standard (25.5 ppb in N_2) on each measurement day was sufficient to calibrate the system.

All measurements were made between 10:00 a.m. and 3.00 p.m., and measurements on each leaf were made at the same time each day (\pm one hour). All measurements were made under the same standard conditions: T of 28°C , PAR of $800 \mu\text{mol m}^{-2} \text{s}^{-1}$ and air flow of $400 \mu\text{mol s}^{-1}$. After a leaf was placed in the cuvette, a minimum of 10 min was allowed for equilibration, and all measurements were made after steady-state conditions were realised, as indicated by continuous monitoring of CO_2 and H_2O fluxes.

2.6. Statistical analyses

In order to analyse the data, the experiment was considered as two cycles: cycle I (21 March–2 April) and cycle II (18 April–8 May), each comprising a drought and a recovery phase. All data analyses were done with SAS software (SAS Institute Inc., Cary, NC, 1995). Results of the whole experiment were analysed using a multivariate analysis of variance (MANOVA). For A and g_s , data were transformed into logarithms to satisfy the assumption of homogeneity of variance. To take into account the overall effect during the course of the experiment, data were first analysed using a two-way ANOVA with repeated measures with drought as a factor (proc GLM) where treatment, time and their interaction were considered. When this test was significant at a 5% level of probability, a single ANOVA was used to test specific differences on each date. Linear and nonlinear regressions (Proc NLIN) were used to determine the relationships between different physiological variables. Values in the text are reported as means ± 1 standard error (SE).

3. Results

3.1. Growth conditions

Inside the phytotron, plants were grown under a 12 h day (from 7:00 a.m. to 7:00 p.m.) and a PAR of $333 \pm 4 \mu\text{mol m}^{-2} \text{s}^{-1}$ ($n = 48$) with average maximum of $511 \pm 17 \mu\text{mol m}^{-2} \text{s}^{-1}$ ($n = 48$) (Fig. 1A). T_{leaf} for T

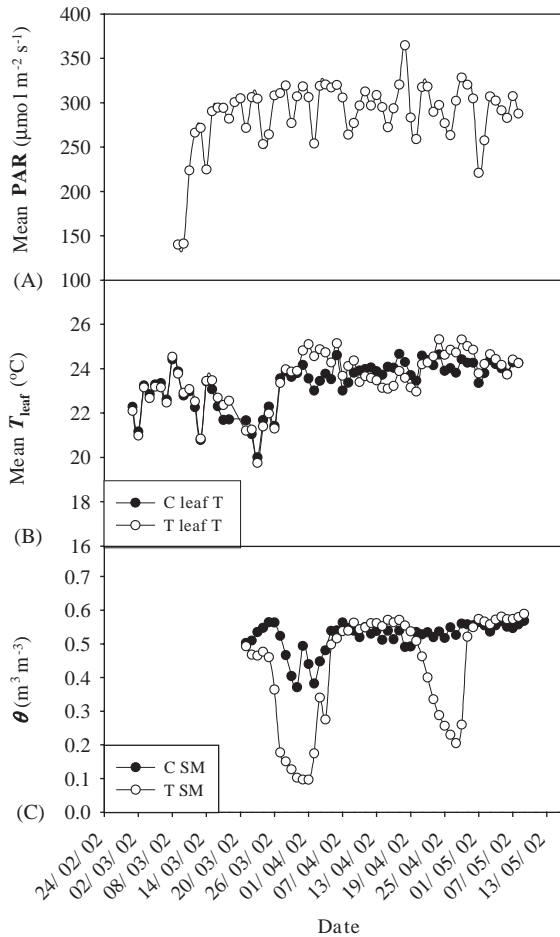


Fig. 1. Growth conditions inside the phytotron during the experiment: daylight average photosynthetic active radiation (PAR) (A) and leaf temperature (T_{leaf}) (B), and 24 h average of soil volumetric water content (θ) (C) for T and C plants.

and C plants was on average $22.9 \pm 0.9^{\circ}\text{C}$ ($n = 48$). During the two periods of drought stress, T_{leaf} of the T plants tended to be higher than T_{leaf} of the C plants as a consequence of the reduced cooling effect of transpiration (Fig. 1B). During March, there were two strong temperature declines caused by the extreme external weather (snowstorms). These temperature drops affected the phytotron internal temperature and clearly influenced T_{leaf} as shown in Fig. 1B. Towards the end of March, temperatures increased and remained stable in the phytotron during the whole period of the experiment. The θ measured for the C plants was on average $0.5 \pm 0.005 \text{ m}^3 \text{ m}^{-3}$ ($n = 38$). During the two drought periods, θ decreased to less than $0.1 \text{ m}^3 \text{ m}^{-3}$ in the first cycle, and to ca. $0.2 \text{ m}^3 \text{ m}^{-3}$ in the second cycle in the T plants (Fig. 1C).

3.2. Drought effect on leaf isoprene emission and gas-exchange parameters

At the beginning of the experiment (21 March, day 0), there was no significant difference (all $P > 0.05$) in θ (ca. $0.45 \text{ m}^3 \text{ m}^{-3}$), F_{iso} (ca. $17 \text{ nmol m}^{-2} \text{ s}^{-1}$) and gas exchange parameters (A : ca. $5.6 \mu\text{mol m}^{-2} \text{ s}^{-1}$; g_s : ca. $0.048 \text{ mol m}^{-2} \text{ s}^{-1}$) between T and C plants (Fig. 2). In the T plants, after 6 days of treatment, θ was reduced to ca. $0.1 \text{ m}^3 \text{ m}^{-3}$ (Fig. 2A). Drought strongly decreased A and g_s to $1.94 \pm 0.55 \mu\text{mol m}^{-2} \text{ s}^{-1}$ and $0.013 \pm 0.002 \text{ mol m}^{-2} \text{ s}^{-1}$, respectively on day 6 (Fig. 2B and C), while F_{iso} remained essentially constant until day 6 at approximately $16.5 \pm 2.1 \text{ nmol m}^{-2} \text{ s}^{-1}$ (Fig. 2D). F_{iso} started to decline daily from day 8 of the experiment when θ was less than $0.1 \text{ m}^3 \text{ m}^{-3}$ and ψ_{PD} was ca. -1 MPa . The isoprene emission rate decreased to $6.2 \pm 1.1 \text{ nmol m}^{-2} \text{ s}^{-1}$ at the end of the first drying cycle on day 12, with a ψ_{PD} of ca. -2 MPa . In contrast to the slow decline in the F_{iso} over time, A and g_s decreased very rapidly from day 2 to almost zero on day 8, and remained essentially constant until day 14. Both A and g_s tracked the decline in θ (although with a one day lag period).

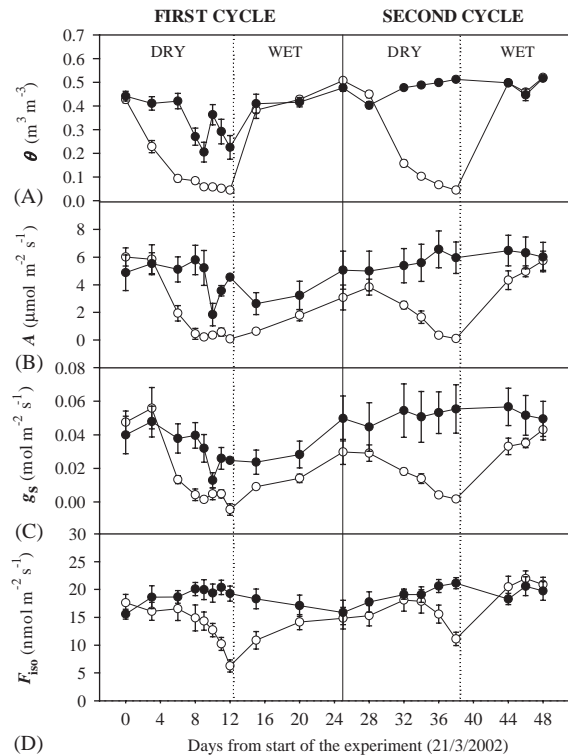


Fig. 2. Time course of isoprene emission rates (F_{iso}) (A), photosynthetic rates (A) (B), stomatal conductance (g_s) (C) and soil volumetric water content (θ) (D) during the first and second drying-rewatering cycles. Each point is the mean $\pm \text{SE}$ ($n = 6$).

In the C plants F_{iso} remained essentially constant at ca. $18 \text{ nmol m}^{-2} \text{ s}^{-1}$. A and g_s dropped from $5.8 \pm 1.0 \mu\text{mol m}^{-2} \text{ s}^{-1}$ and $0.040 \pm 0.007 \text{ mol m}^{-2} \text{ s}^{-1}$, respectively on day 8 to $1.8 \pm 0.8 \mu\text{mol m}^{-2} \text{ s}^{-1}$ and $0.013 \pm 0.004 \text{ mol m}^{-2} \text{ s}^{-1}$ on day 10, as a consequence of a small drought stress. θ decreased from 0.42 ± 0.03 to $0.20 \pm 0.04 \text{ m}^3 \text{ m}^{-3}$ during the 3 day interval between day 6 and day 9 during which the C plants were not watered. During the 16-day recovery period (from day 12 to day 28), F_{iso} recovered quickly upon re-watering, reaching the C emission rate (ca. $15 \text{ nmol m}^{-2} \text{ s}^{-1}$) on day 13. A and g_s still showed a slight sign of water-stress at the start of the second cycle, but the differences between T and C plants on day 16 were not significant ($P > 0.05$).

During the second drought period, from day 28 to day 38, θ decreased from 0.45 ± 0.01 to $0.045 \pm 0.007 \text{ m}^3 \text{ m}^{-3}$ (Fig. 2A). Similarly to the first cycle, in the second cycle A and g_s decreased at a faster rate than F_{iso} , which began to decline later, reaching values of $0.10 \pm 0.01 \mu\text{mol m}^{-2} \text{ s}^{-1}$, $0.0020 \pm 0.0002 \text{ mol m}^{-2} \text{ s}^{-1}$ and $11.1 \pm 1.2 \text{ nmol m}^{-2} \text{ s}^{-1}$, respectively by day 38 (Fig. 2B, C and D). In the second recovery period F_{iso} from T plants reached C emission rates on day 44 at ca. $20.5 \text{ nmol m}^{-2} \text{ s}^{-1}$, with θ having recovered to ca. $0.5 \text{ m}^3 \text{ m}^{-3}$. A and g_s from the T plants recovered to C plant values by day 48 at ca. $5.74 \mu\text{mol m}^{-2} \text{ s}^{-1}$ and ca. $0.043 \text{ mol m}^{-2} \text{ s}^{-1}$, respectively. In the C plants, A , g_s and F_{iso} remained essentially stable at ca. $5.9 \mu\text{mol m}^{-2} \text{ s}^{-1}$, $0.05 \text{ mol m}^{-2} \text{ s}^{-1}$ and $19.5 \text{ nmol m}^{-2} \text{ s}^{-1}$, respectively. θ remained essentially constant at ca. $0.48 \text{ m}^3 \text{ m}^{-3}$.

At the beginning and the end of the experiment and during the recovery period, the C_{iso}/C_A was only around 2%. During the two severe water-stress periods when A was less than $0.5 \mu\text{mol m}^{-2} \text{ s}^{-1}$, the C_{iso}/C_A reached values as high as 50%. Because these values were obtained when A was close to zero, calculations may have been somewhat misleading. However, for values of A larger than $0.5 \mu\text{mol m}^{-2} \text{ s}^{-1}$, the C_{iso}/C_A still increased significantly with decreasing θ (Fig. 3). In the C plants the C_{iso}/C_A remained essentially constant at ca. 2%, with the exception of a rapid increase to values of ca. 5% reached in response to the slight water-stress that the C plants suffered during the first cycle.

During the two consecutive cycles there was a significant difference between the response of F_{iso} and that of A to changes in θ , g_s and ψ_{PD} ($P > 0.01$ in all cases for the repeated measures analysis). Although F_{iso} responded to water-stress later and more slowly than A , both showed a distinctive response to θ during the drought period and the recovery period (Fig. 4A and B). For equivalent θ , both isoprene and assimilation showed higher rates during the drought phase than during the recovery phase. F_{iso} did not show any relationship to g_s for g_s values higher than $0.02 \text{ mol m}^{-2} \text{ s}^{-1}$. Only when g_s decreased below $0.02 \text{ mol m}^{-2} \text{ s}^{-1}$ in the T plants F_{iso}

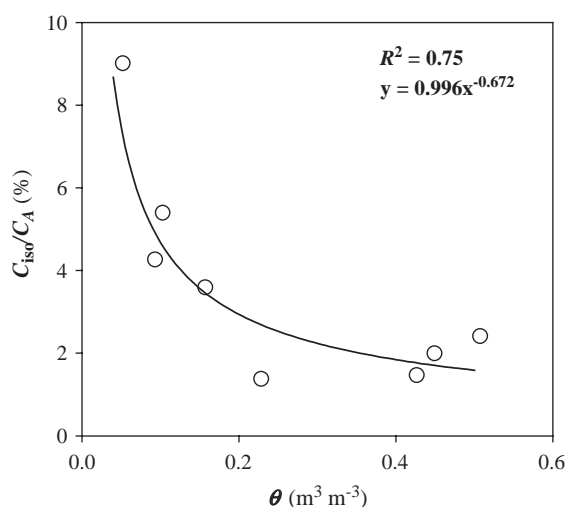


Fig. 3. Relationship between the percentage of assimilated C emitted as isoprene (C_{iso}/C_A) and soil volumetric water content (θ) for the T plants during the dry periods. C_{iso}/C_A is shown only for days in which photosynthetic rate (A) was > 0.5 . Each point represents the mean of six replicates.

dropped dramatically (Fig. 4C). As expected, and opposite to F_{iso} , A showed a strong linear correlation with g_s ($R^2 = 0.93$) for both T and C plants (Fig. 4D). F_{iso} only started to decline when A was already reduced by as much as 90% which corresponded to a C_{iso}/C_A of ca. 10% (Fig. 4E and 4F). F_{iso} dropped significantly when the C cost to the plant for isoprene emission was very high, i.e. during the most severe period of the drought when A was reduced almost to zero.

The effect of decreasing ψ_{PD} on A was very strong (Fig. 5A), with A immediately reduced to zero when ψ_{PD} reached ca. -1 MPa . F_{iso} and ψ_{PD} showed a well-correlated ($R^2 = 0.64$) linear negative trend (Fig. 5B). The negative effect was not as pronounced as for A , probably as a result of the little effect stomata have in controlling F_{iso} from leaves (Fall and Monson, 1992). The relationship between F_{iso} and A for the T plants over the duration of the experiment, divided into drought period and watered period, is shown in Fig. 6. F_{iso} during drought did not decline much until A was very low and was characterised by a faster recovery during the rewatering period.

4. Discussion

Our results indicate that although F_{iso} decreased when the water-stress was severe, it was considerably less sensitive to drought than A and g_s (Tingey et al., 1981; Sharkey and Loreto, 1993; Fang et al., 1996; Lerdau et al., 1997; Guenther et al., 1999; Bruggemann and Schnitzler, 2002). It was also apparent that F_{iso} could

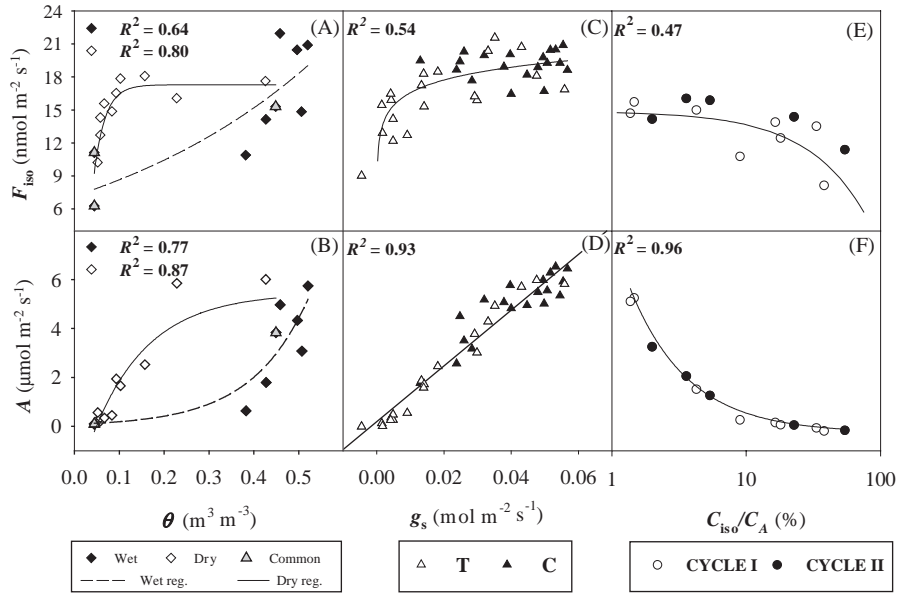


Fig. 4. Relationship of isoprene emission rates (F_{iso}) and photosynthetic rates (A) with soil volumetric water content (θ) (A and B), stomatal conductance (g_s) (C and D) and the percentage of assimilated C emitted as isoprene (C_{iso}/C_A) (E and F). Each point represents the mean of six replicates. In (A) and (B) symbols represent the T plants during the dry (white diamonds) and the wet (well-watered and recovery) (black diamonds) periods over the whole experiment (two cycles). The “Common” points (grey triangles) correspond to the transition between one phase and the next one. Curves have been drawn only for a better illustration of the trend. In (C) and (D) symbols represent the T (white triangles) and C (black triangles) plants over the whole experiment (two cycles). In (E) and (F) symbols represents the T plants during the drought phase of the first (white dots) and the second (black dots) cycle. Note that the abscissa scale is logarithmic.

recover from water-stress much more quickly than A and g_s . Furthermore, we observed for the first time that for equivalent θ both isoprene emission and assimilation appear to have higher rates during the drying phase than during the recovery phase. Unlike A , the response of F_{iso} to drought appears to be independent of stomatal dynamics (Tingey et al., 1981; Fall and Monson, 1992; Fang et al., 1996). In the short-term, during the drought phase, even though g_s was drastically reduced over an eight day period, were F_{iso} remained essentially constant. Only when g_s decreased below ca. $0.01 \text{ mol m}^{-2} \text{ s}^{-1}$, F_{iso} drastically reduced. This finding suggests that g_s did not control F_{iso} and that an internal factor controlled the decrease in the emission rate when the water-stress was severe. In the short-term, F_{iso} also appeared not to be directly dependent on A . Although most of the C in isoprene (between 72% and 91%) is derived from recent photosynthate, it has been observed that plants also use alternative, slow turn-over, sources (Sharkey et al., 1991; Affek and Yakir, 2003; Delwiche and Sharkey, 1993; Karl et al., 2002; Funk et al., 2004; Schnitzler et al., 2004). Moreover, it has been found that under stress conditions plants may increase the relative contribution of this alternative C to over 30% to maintain high F_{iso} when A are inhibited (Funk et al., 2004; Schnitzler et al., 2004). Although in the current

study it was not possible to quantify the relative contribution of fresh photosynthate and slow turn-over alternative sources, our results are consistent with these findings. It is likely that F_{iso} started to decline when the C_{iso}/C_A was only 10% because the slow turn-over alternative C sources did not provide enough C. The drop of F_{iso} after a period of severe water-stress may be the result of the depletion of these alternative sources.

Furthermore, drought stress appeared to have a profound influence on the percentage of C_{iso}/C_A . Previous studies showed that in non-water-stressed plants ca. 1–2% of the photosynthetically fixed C is emitted as isoprene (Sharkey et al., 1991; Baldocchi et al., 1995; Monson and Fall, 1989; Harley et al., 1999), whereas under stress conditions (water-stress, high-temperature, etc.) C_{iso}/C_A may exceed 30% (Sharkey and Loreto, 1993; Fang et al., 1996). During the current study, we found a C_{iso}/C_A for the C plants of ca. 2%. In the T plants, the proportion of C lost as isoprene increased during water-stress periods, with peak values that exceeded 50%. These peaks were the result of a major reduction in A (close to zero) while F_{iso} remained high. However, the percentage of C lost as isoprene clearly increased from the beginning through the whole drought period showing a good relationship with θ . Because of the strong dependence of F_{iso} on leaf

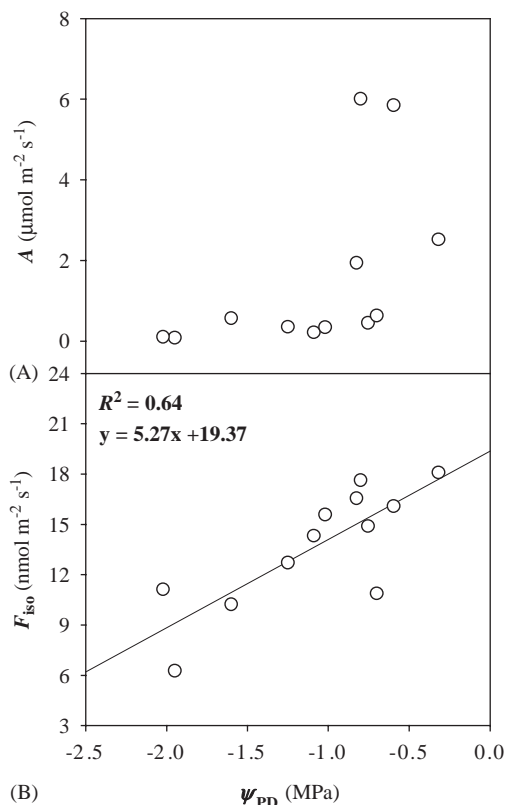


Fig. 5. Relationship between photosynthetic rates (A) (A) and isoprene emission rates (F_{iso}) (B), and pre-dawn leaf water potential (ψ_{PD}) for the T plants during the whole experiment (two cycles).

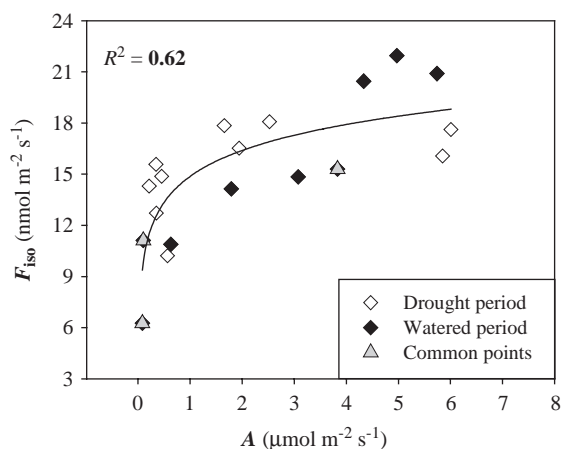


Fig. 6. Relationship between isoprene emission rates (F_{iso}) and photosynthetic rates (A) for the T plants during the dry (white diamonds) and wet (well-watered and recovery) (black diamonds) periods, over the whole experiment (two cycles). The “Common points” (grey triangles) represent the transition days between one phase and the next one. Each point represents the average of six replicates.

temperature, this C loss may become even larger in areas with warm climate where drought-induced stomatal closure may have a large indirect effect on F_{iso} by increasing leaf temperature.

In a climate change scenario with higher temperatures and prolonged droughts, the ratio of F_{iso} to A could dramatically increase with significant impact on the global terrestrial C balance, especially in regions such as the tropics which are estimated to contribute more than 80% of the annual isoprene flux (Jacob and Wofsy, 1988; Zimmerman et al., 1988; Guenther et al., 1995). Although many studies have been published over the past 10 years on F_{iso} by plants, additional research focusing on water-stress using a range of species is needed in order to enable us to model plant F_{iso} response to drought in different climate scenarios. It is desirable to relate biogenic emissions to measurable physiological parameters that control emission variations. ψ_{PD} is the most likely candidate for describing the role of water limitations on biogenic emissions from leaves and there are several vegetation models that can be used to predict it. This parameter also may be needed for estimating accurate T_{leaf} during drought conditions. As our results suggest, there may exist a tight relationship between F_{iso} and ψ_{PD} during water-stress episodes. Although it is likely that the slope of the relationship between ψ_{PD} and F_{iso} varies widely between species, we believe that ψ_{PD} could be a useful parameter to include in isoprene emission models to account for effects of drought stress. Although measured under controlled conditions, the observed values of ψ_{PD} in this study are similar to those observed for oak species in the field during summer natural drought conditions (Martinez-Vilalta et al., 2003; Bombelli and Gratani, 2003; Owens and Schreiber, 1992). The coefficient of the relationship between F_{iso} and ψ_{PD} reported in this study could therefore be used by modellers to set up a first model parameterisation that could be improved upon in the future.

Finally, investigations using potted plants and laboratory measurements provide valuable information from which to build hypotheses, but these studies often yield results that differ from those observed using field-grown adult plants in their natural environment. There is therefore a strong need for further field studies to test any definitive model for the F_{iso} response to water-stress in natural ecosystems.

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