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The key-role of topsoil moisture on CO₂ efflux from a Mediterranean *Quercus ilex* forest

Richard JOFFRE^{a*}, Jean-Marc OURCIVAL^a, Serge RAMBAL^a, Alain ROCHETEAU^{a,b}

^a Équipe DREAM, CEFÉ-CNRS, 1919 Route de Mende, 34293 Montpellier Cedex 5, France

^b UR CLIFA, IRD-CNRS, 1919 Route de Mende, 34293 Montpellier Cedex 5, France

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Abstract – CO₂ respiratory losses partly determine net carbon ecosystem exchanges. The main objective of this paper was to understand regulation imposed by soil water content and temperature on soil and ecosystem CO₂ efflux in a holm oak (*Quercus ilex* L.) Mediterranean forest. Soil CO₂ efflux was monitored monthly during 1999 and 2001. Moreover, experimental water treatments were conducted in 1999 over 9 small plots (0.3 m²) during nine months. Results showed strong decreases of soil CO₂ efflux for a relative soil water content below 0.7. Ecosystem respiration measured by eddy covariance over a 4-year period showed strong sensitivity to soil water content and temperature. Severe limitations of soil and ecosystem efflux imposed by low values of soil water content occurred on about 90 days per year. The best adjustments of soil and ecosystem CO₂ efflux were obtained using regression models where the exponential effect of temperature is linearly related to soil water content ($r^2 = 0.68$ and 0.79 for soil and ecosystem respectively). Our results highlighted strong differences in respiration sensitivity to topsoil moisture between soil and ecosystem. When the relative water content (RWC) is low (0.4), an increase of 1 °C provokes an increase of soil respiration of 5.7% and an increase of ecosystem respiration of 8.6%. For nonlimiting soil water conditions, at RWC = 1, the increases of respiration caused by a 1 °C temperature increase are of 8.5% and 16.5% for soil and ecosystem respectively. These results emphasized the probable determinant influences of changes in soil water regime for respiratory fluxes and net carbon exchanges of Mediterranean forest ecosystems.

CO₂ efflux / soil water content / soil temperature / ecosystem respiration / Mediterranean ecosystem / *Quercus ilex*

Résumé – Le rôle-clé de l'humidité du sol superficiel sur les efflux de CO₂ d'une forêt méditerranéenne de chêne vert. Les pertes de CO₂ par respiration vont déterminer largement les échanges nets de carbone des écosystèmes. L'objectif principal de cet article est de comprendre les régulations imposées par la teneur en eau et la température du sol sur les efflux de CO₂ du sol et de l'écosystème dans une forêt méditerranéenne de chêne vert (*Quercus ilex* L.). La respiration du sol a été mesurée mensuellement en 1999 et 2001. Par ailleurs, une expérimentation, mise en place en 1999, comprenant trois régimes hydriques a été suivie pendant 9 mois sur 9 parcelles de 0.3 m². Les résultats mettent en évidence la très forte limitation des efflux lorsque la teneur en eau du sol est inférieure à 70 % de sa capacité de rétention. La respiration de l'écosystème mesurée sur une période de 4 ans par la méthode des fluctuations turbulentes montre la même sensibilité aux deux facteurs. Les conditions de fortes limitations par une faible teneur en eau du sol affectent l'écosystème environ 90 jours par an. Les meilleurs ajustements pour la simulation des flux de CO₂ du sol et de l'écosystème sont obtenus pour un modèle dans lequel l'effet exponentiel de la température est fonction linéaire de la teneur en eau du sol (r^2 de 0.68 et 0.79 pour le sol et l'écosystème). La sensibilité de la respiration à la teneur en eau du sol est plus grande pour le sol que l'écosystème. En conditions hydriques sèches, pour une capacité relative en eau (RWC) égale à 0.4, une augmentation de température de 1 °C entraîne une augmentation de la respiration du sol et de celle de l'écosystème de 5.7 % et de 8.6 % respectivement. En conditions non limitantes (RWC = 1), le même accroissement de température provoque une augmentation de respiration de 8.5 % et 16.5 % pour le sol et l'écosystème respectivement. Toute modification des conditions hydriques aura donc des répercussions sur les flux respiratoires et sur les échanges nets de carbone des écosystèmes forestiers méditerranéens.

flux de CO₂ / humidité du sol / température du sol / respiration de l'écosystème / écosystème méditerranéen / *Quercus ilex*

1. INTRODUCTION

The efflux of CO₂ from the soil, also referred to as soil respiration, is a major component of the global carbon balance [33, 44]. Its importance is equal or greater than the estimated terrestrial net primary production [3, 34]. It represents the main source of all carbon dioxide entering the atmosphere with a

contribution being 20 to 40% of the total flux [22]. The rate at which CO₂ is produced in the soil is largely controlled by soil temperature and water content (e.g. [45]). Global temperature increase could lead to opposite effects on carbon storage: first, an increase of the net primary productivity and the input of organic carbon in the soils, and second, a stimulation of organic matter decomposition increasing the loss of soil

* Corresponding author: joffre@cefe.cnrs-mop.fr

organic carbon which in turns lead to an increase of atmospheric CO₂ with probable influence on air temperature by feedback effect [19]. Soil moisture constitutes the second factor regulating the soil CO₂ efflux, by limiting the respiration when dry conditions occur [17]. Nevertheless, interactions between soil temperature and soil moisture are non linear. A change in soil moisture has a greater impact when the temperatures are higher while a change in temperatures has a greater impact when the soil is humid [18].

Various models have been proposed to describe soil respiration. They are generally based on temperature-dependent relations [21, 23, 25, 42], combined with soil moisture [9, 11, 13, 16]. Most of the models that take into account temperature and soil moisture at the same time, assumed that the effects are multiplicative whereas some of them let vary the effect of temperature with soil moisture [9, 37]. The seasonality of Mediterranean climates characterised by strong variations of soil temperature and soil moisture offers a unique opportunity to study the temporal changes in CO₂ efflux in response to soil water availability and temperature.

Several data are available on the respiration of Mediterranean ecosystems. Most of them were measured in the Mediterranean Basin [4, 5, 10, 15, 26, 32, 37, 38]. Some other data dealing with Australian ecosystems under Mediterranean climate are also available [12, 29]. They all highlight the effect of the summer drought on soil respiration and some of them also show the negative effect of the cold temperature in winter on respiration. Two types of measurements were involved in the present study. First, hourly ecosystem respiration was measured using the eddy covariance technique [1, 2] over extensive period of several months in order to cover a large array of soil moisture and temperature conditions. Second, soil respiration measurements were conducted over a large array of temperature and soil moisture obtained through the design of an original experiment combining three contrasted treatments (control, dry and wet). Our main objective was to describe the effects of soil moisture and temperature on soil and ecosystem respiration considering both net ecosystem CO₂ exchange using eddy covariance and soil CO₂ efflux measured with a soil respiration chamber. Further, we tested the effects of soil moisture on temperature sensitivity for both soil respiration and ecosystem respiration.

2. MATERIALS AND METHODS

2.1. Study site

The study site is located 35 km NW of Montpellier (southern France) in the Puéchabon State Forest (3° 35' 45" E, 43° 44' 29" N, elevation 270 m). This forest has been managed as a coppice for centuries and the last clear cut was performed in 1942. Vegetation is largely dominated by the overstorey tree *Quercus ilex* L. whose cover is larger than 80% and has a leaf area index of 2.96 [20]. Mean tree height was about 5.5 m. In 2001, the density of sprouted stems was 7149 stems per ha. The percentages of stem with DBH < 4 cm and DBH > 7 cm were 12% and 46% respectively. The above-ground biomass was about 11 300 ± 2800 g dry matter (DM) m⁻². Understorey species compose a sparse (percent cover lower than 25) shrubby < 2 m layer with *Buxus sempervirens* L., *Phyllirea latifolia* L., *Pistacia terebinthus* L. and *Juniperus oxycedrus* L. The mean annual lit-

terfall was 428 ± 30 g DM m⁻² (leaf = 254 ± 58 g DM m⁻²) and the current annual growth increment was 185 g DM m⁻². Consequently the aboveground net productivity (ANPP) is about 613 g DM m⁻² [36].

The area has a Mediterranean-type climate. Rainfall occurs during autumn and winter with about 75% between September and April. Mean annual precipitation over the previous 18 years is 883 mm with a range of 550–1549 mm. Mean annual temperature over the same period is 13.5 °C. This forest grows on hard Jurassic limestone. The soil is classified as calcareous fersiallitic soil (or rhodo-chromic luvisol according to the FAO classification) with high clay (39.6%) and low sand content (14.1%) in the 0–50 cm layer [26]. The averaged volumetric fractional content of stones and rocks is about 0.75 for the top 0–50 cm and 0.90 for the whole profile leading to a maximum available water of 150 mm cumulated over 4.5 m depth (Rambal unpublished data).

2.2. Experimental design of the instantaneous soil CO₂ efflux measurements

Nine randomly distributed permanent plots were delimited within a 30 × 30 m area in December 1998. At each plot, metal frames (55 × 55 cm) were inserted into the soil at 5 cm depth to avoid water infiltration through surface runoff. Three plots corresponding to the dry treatment (D) were protected from the rain using a PVC roof installed 20 cm above the forest floor. Three other plots were not covered and corresponded to the control treatment (C) submitted to the current rainfall regime. The last 3 plots corresponding to the wet treatment (W) were irrigated and maintained near to field capacity. Twice a week, the litter fallen on the PVC roof of the D- and W-plots was replaced inside the plot on the soil surface. In situ soil CO₂ efflux R_{soil} was measured using a dynamic-closed system based on an infrared gas analyzer (ADC LCA2, Analytical Development Company, UK). Air was pumped (60 cm³ min⁻¹) from the sample chamber (volume 300 cm³, area 33 cm²) to the IRGA detector and then back into the chamber in a closed loop. The change in CO₂ concentration over time yields an estimate of soil respiration. The system was allowed to equilibrate with ambient air before measurements. The chamber was placed on the soil and held firmly. A first reading was taken after 30 s to let the CO₂ value stabilize. After 60 s a second reading was taken, the CO₂ efflux being calculated as the difference between the two measurements. Measurements were done between January and October 1999, 10 times for the dry and wet treatments and 16 times for the control treatment. Three measurements were performed in each permanent plot and averaged. In order to normalise our measurements with those conducted with the LiCor dynamic closed system (Chamber Li6400-09 coupled with the LiCor 6400 IRGA), an intercalibration between both systems was conducted in June 2000 giving us the following corrective equation $R_{sLicor} = 0.4735 * R_{sADC} - 0.12$ ($r^2 = 0.87$, $n = 85$). All the data measured with the ADC were consequently corrected using this equation. Additional measurements of 4 control plots were monthly done during the year 2001 using the LiCor dynamic closed system. A two-way Anova, testing the effects of treatment and plot, was performed for each date of measurements.

2.3. Soil temperature and soil moisture

In each plot, soil temperature at 15-cm soil depth was measured every 5 min using a copper–constantan thermocouple (Type T). Data were recorded with a data-logger (Model 21X, Campbell Scientific Ltd.) and processed to calculate average hourly values. Soil moisture was measured with TDR (Trase USA, Model 6050X1) with two pairs of 15-cm probes in each plot. Measurements were done once a week.

For the D and W treatment soil moisture was interpolated between two successive measurements. To have a continuous set of soil water

content for the C treatment, rather than interpolating the discrete TDR values, we used a daily soil water balance model. We assumed the topsoil water to be only influenced by infiltrated rainfall and soil evaporation. Soil evaporation was calculated in two stages: (1) the constant rate stage, when the supply of energy to the surface limits evaporation, and (2) the falling rate stage when water movement to the evaporating surface is controlled by the soil hydraulic properties. Details for calculating soil evaporation are given by Ritchie [39]. In stage 1, the soil was sufficiently wet for water to be transported to the surface at a rate equal to the rate of potential soil evaporation. During stage 2, according to diffusion theory, cumulative evaporation (in this stage) is proportional to the square root of the elapsed time after the beginning of this stage. Soil evaporation parameters were 10 mm for the upper limit of first stage evaporation and 4.5 mm d^{-1/2} for the second stage coefficient. These parameters were the same as those used by Rambal [35] for a similar soil.

2.4. Eddy covariance measurements of ecosystem CO₂ efflux

A 11 m height tower with a 2 m mast was installed in the middle of the stand in June 1998. Wind speed components were measured with an Ultrasonic 3D anemometer (Solent R2, Gill Instruments, Lymington, UK) installed on the top of the mast, i.e. 7 m above the tree canopy. Air was sampled at the base of the sonic anemometer through a 0.2 µm filter (PTFE Acro 50, Gelman) and pumped at a flow rate of 1.5 10⁻⁴ m³ s⁻¹. Water vapour and carbon dioxide concentration were measured with a LI-6262 IRGA analyser (Li-Cor, Lincoln, NE, USA) placed on the tower, 2 m below the sonic anemometer. Wind speed and gas concentrations were scanned at a frequency of 21 Hz. The IRGA analyser was recalibrated every 3 weeks for CO₂ and every 7 weeks for H₂O. The flow rate of N₂ in the reference cell was 3.3 10⁻⁷ m³ s⁻¹. CO₂ fluxes were computed using Edisol software [27] and following the corrections described in [1].

Ecosystem respiration could be estimated by night-time eddy covariance fluxes under some specific conditions of turbulence to eliminate stable night-time conditions leading to CO₂ storage in the layer below the eddy flux system. To avoid underestimation due to CO₂ storage, we plotted night-time fluxes against friction velocity u^* [1] and determined the value of u^* beyond which CO₂ fluxes did not depend of u^* . Above this threshold, 0.35 m s⁻¹ in our site, storage may be considered as negligible and CO₂ flux equals ecosystem respiration. The threshold determined at Puéchabon was close to the values determined at many Euroflux sites [1]. Moreover, we selected nights where at least 6 consecutive half-hour periods presented u^* values equal or higher than 0.35 m s⁻¹. To avoid interference with growth respiration, we analysed data collected out of the vegetation growth period (from March to June). Over the period of study (July 1998 to November 1999 and July 2000 to December 2001), 302 nights satisfied these conditions and were consequently considered for ecosystem respiration estimation.

2.5. Data treatment

Soil respiration (R_s) and ecosystem respiration (R_{eco}) were modelled using three classes of models. The first one involves only soil temperature using an exponential function (model 'Temp')

$$R_s = R_{s,ref} \cdot e^{b(T - T_{ref})/10} \quad (1a)$$

$$R_{eco} = R_{eco,ref} \cdot e^{b(T - T_{ref})/10} \quad (1b)$$

with T = soil temperature at 15-cm depth, $R_{s,ref}$ and $R_{eco,ref}$ being the respiration under standard conditions (at T_{ref}).

In the second type of model, respiration is modelled considering a multiplicative dependency on soil temperature and soil moisture (model 'Multi'):

$$R_s = R_{s,ref} \cdot f(\theta) \cdot e^{b(T - T_{ref})/10} \quad (2a)$$

$$R_{eco} = R_{eco,ref} \cdot f(\theta) \cdot e^{b(T - T_{ref})/10} \quad (2b)$$

with T = soil temperature at 15-cm depth, $R_{s,ref}$ and $R_{eco,ref}$ being the respiration under standard conditions (at T_{ref} and nonlimiting soil moisture). $f(\theta)$ was expressed in two different ways:

as percent of soil water content at field capacity (RWC) (Eq. (3))

$$f(\theta) = RWC = \frac{\theta}{\theta_{fc}} \quad (3)$$

with θ current soil water content and θ_{fc} soil water content at field capacity, that is θ measured after a large rain event and two draining days;

or as soil matrix potential through a Campbell-type equation (Eq. (4)) [7, 8] for representing the soil moisture characteristic or retention curve linking potential and soil water content

$$f(\theta) = \psi_{fc} RWC^b \quad (4)$$

with ψ_{fc} potential at field capacity, i.e. at a pressure value of -33 kPa. The exponent b was calculated from the pedotransfer function proposed by [43].

In the third model, the rate constant of temperature is a linear function of soil moisture (model 'Expo'):

$$R_s = R_{s,ref} \cdot f(\theta) \cdot e^{(b f(\theta) + c)(T - T_{ref})/10} \quad (5a)$$

$$R_{eco} = R_{eco,ref} \cdot f(\theta) \cdot e^{(b f(\theta) + c)(T - T_{ref})/10} \quad (5b)$$

with T , $R_{s,ref}$, $R_{eco,ref}$ and $f(\theta)$ as in equations (2a) and (2b).

T_{ref} was fixed in all models at 0 °C.

To take into account a possible delay between the rapid modification of soil moisture after rainfall and the induced flush of microbial respiration, moisture contents over different periods of time were calculated and tested. Five adjustments corresponding to soil moisture measured on the day of measurement (RWC_1), or mean values calculated over 2 (RWC_{12}), 3 (RWC_{13}), 4 (RWC_{14}), and 5 (RWC_{15}) days before this day were performed. For the ecosystem respiration measurements, the soil temperature corresponded to the average of night-time soil temperature. Parameters were estimated using a non-linear regression procedure (NLIN) of SAS software. Fits of the different models were evaluated by calculating the adjusted coefficient of determination and the root mean squared error (RMSE). For each model, we selected the best two combinations of variables for the expression of soil moisture.

3. RESULTS

3.1. Soil RWC and soil temperature

During the 1999 experiment, soil RWC ranged from 0.46 and 0.51 for the D treatment and from 0.76 and 0.93 for the W treatment. Fluctuations of RWC were larger for the C ranging during the experiment from 0.45 to 0.94 (Fig. 1b). Water manipulation in the experimental plots allowed measurements of soil CO₂ efflux in dry and cold conditions in winter.

Time-course of topsoil RWC over the four years of monitoring showed important seasonal variations whose general pattern is characteristic of the Mediterranean climate (Fig. 2).

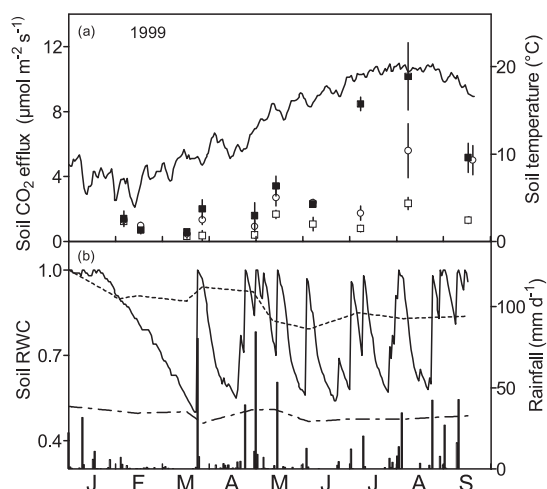


Figure 1. Time course of meteorological conditions and observed soil CO₂ efflux during the 1999 experiment. (a) Daily soil temperature (0–15 cm depth) and soil CO₂ efflux, open squares correspond to the dry treatment, open circles to the control and closed squares to the wet treatment (vertical bars indicate standard error of the mean). (b) Daily rainfall and upper layer (0–15 cm depth) soil relative water content (RWC), solid line corresponds to control, dashed line to wet treatment, dot-dashed line to dry treatment.

Strong interannual variability affected autumnal recharge. As a consequence, winter field capacity could be reached early, as in 1999 and 2000, or very late as in 2001 and 1998. Winter drought could be marked as in 1999 and 2000 with RWC reaching low values around 0.5. Strong daily rainfall events during summer (as in 1999) could modify substantially the length of summer drought.

Mean daily soil temperatures ranged from 3.9 °C to 20.5 °C during the water manipulation experiment and were not significantly different between the 3 treatments. The PVC roofs installed over the dry plots to avoid the infiltration of rainfall provoked a maximum difference of daily soil temperature of 0.2 °C as compared to control. Ecosystem respiration was measured over a quite similar range of temperatures from 2.79 °C to 23.1 °C.

3.2. Soil CO₂ efflux during the field experiment

Mean values of soil CO₂ efflux ranged from 0.47 to 5.59 μmol m⁻² s⁻¹ for C, from 0.31 to 2.34 μmol m⁻² s⁻¹ for the D treatment and from 0.58 to the 10.16 μmol m⁻² s⁻¹ for the W treatment (Fig. 1a). Over the experiment, the soil CO₂ efflux increased by a factor 18 for the W, 12 for the C and 7 for the D treatment when soil temperature varied by a factor 5 from 3.9 to 20.5 °C. All treatments experienced low values when soil temperature was less than 7 °C (mean ratio of CO₂ efflux between D and C plots was 0.86 for the February values). Differences increased with soil temperature over spring and summer and were the highest when soil temperature exceeded 17 °C (mean ratio of CO₂ efflux between D and C plots = 0.40 for the last 4 dates). During the low temperature period (from February to mid-March), the efflux were not significantly different between treatments. From the end of

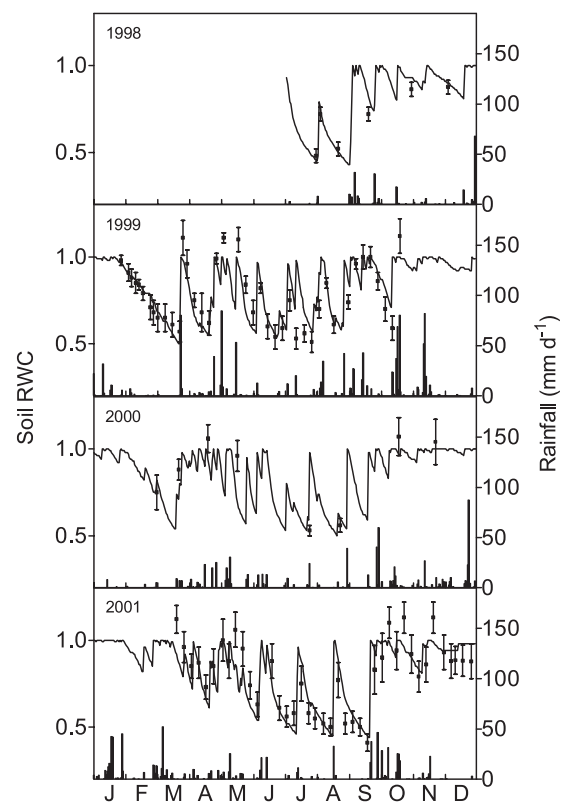


Figure 2. Daily rainfall, modelled (full line) and observed (data points) upper layer (0–15 cm depth) relative soil water content (RWC) during the 1998–2001 period. Vertical bars indicate ± 1 SE.

March (26/03) till the end of the experiment, the treatment effect was highly significant ($P < 0.001$). The plot effect was only significant in July 1999 due to the high heterogeneity of data in the C plots. The interaction treatment \times plot was never significant.

3.3. Ecosystem respiration

Ecosystem respiration ranged from low values close to 1 μmol m⁻² s⁻¹ recorded in dry summer (1998, 2001) and winter when strong limitations were imposed by low soil moisture or low temperature, to high values between 6 and 8 μmol m⁻² s⁻¹ recorded in the wet summer 1999 and in autumn following important rainfall events and when soil temperature was still high (around 17–19 °C) (Fig. 3). It is noteworthy that the first important rainfall (20 mm) in autumn 1998 after the summer drought provoked a 4.5-fold increase in ecosystem respiration between 27 September 1998 (1.16 μmol m⁻² s⁻¹) and 4 October 1998 (5.37 μmol m⁻² s⁻¹). The same pattern of a strong flush was frequently observed during summer 1999 and in autumn 2000 and 2001.

3.4. Model comparison

Independent fit on the three soil treatments respiration values were done in order to compare the adjusted parameters

Table I. Parameter estimates and regression results of soil CO₂ efflux versus soil temperature and soil relative water content (RWC) using equations (1–3) (see text) ($n = 93$). RWC_1 corresponds to the value on the day of respiration measurement, RWC_{15} corresponds to the mean values calculated over 5 days before the day of respiration measurement. $R_{s,ref}$ is the soil respiration under standard conditions (at T_{ref}), $RMSE$ root mean squared error.

Model	Soil moisture variable	$R_{s,ref}$	b	c	r^2	RMSE
Temp (Eq. (1))	–	1.875	0.359		0.06	2.14
Multi (Eq. (2))	RWC_1	1.454	0.759		0.53	1.66
Multi (Eq. (2))	RWC_{15}	1.613	0.685		0.50	1.71
Expo (Eq. (3))	RWC_1	0.551	1.417	0.241	0.68	1.25
Expo (Eq. (3))	RWC_{15}	0.761	1.5058	-0.046	0.65	1.31

Table II. Parameter estimates and regression results of ecosystem CO₂ efflux versus soil temperature and soil water content using equation (1–3) (see text) ($n = 302$). RWC_1 corresponds to the value on the day of respiration measurement, RWC_{15} corresponds to the mean values calculated over 5 days before the day of respiration measurement. $R_{eco,ref}$ is the soil respiration under standard conditions (at T_{ref}), $RMSE$ root mean squared error.

Model	Soil moisture variable	$R_{eco,ref}$	b	c	r^2	RMSE
Temp (Eq. (1))	–	1.635	0.364		0.23	1.04
Multi (Eq. (2))	RWC_1	1.282	0.683		0.72	0.66
Multi (Eq. (2))	RWC_{15}	1.292	0.678		0.66	0.72
Expo (Eq. (3))	RWC_1	1.0625	0.467	0.383	0.79	0.54
Expo (Eq. (3))	RWC_{15}	1.055	0.529	0.367	0.73	0.62

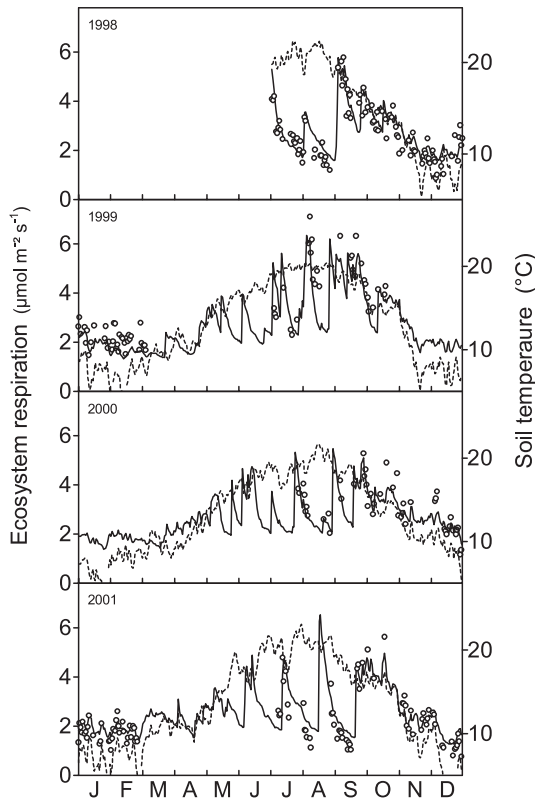


Figure 3. Time course of soil temperature (dashed line), simulated ecosystem respiration (full line) modelled using ‘Expo’ model with RWC_1 and daily measured eddy covariance ecosystem respiration (open circles) during the 1998–2001 period.

between treatments. Due to the small numbers of degree of freedom for the D and W treatments ($n = 10$), and whichever the model under consideration, parameters were adjusted with very large confidence limits. Consequently, the parameters comparison was irrelevant. Pooling soil respiration data from the 3 treatments ($n = 93$) or determining model parameters only on the 1999 C treatment plus the monthly values obtained in 2001 ($n = 73$) did not significantly change the parameters

but increased the $RMSE$ of the models. Tables I and II showed respectively the parameters of the different models on the whole dataset of soil respiration and on ecosystem respiration.

For both measurements, soil CO₂ efflux and ecosystem respiration, the goodness of model fit decreased in the order ‘Temp’ model < ‘Multi’ model < ‘Expo’ model (Tabs. I and II). In all cases, model estimates were better for ecosystem respiration than for soil efflux. The model ‘Temp’ explained only 6% of the variance of the soil efflux and 23% for the ecosystem respiration. Introducing soil moisture in the two other model allows us to better describe the measurements (r^2 ranging from 0.50 to 0.68 for soil efflux and from 0.66 to 0.79 for ecosystem respiration). The ‘Expo’ model gave the best fits whichever variable considered to describe soil moisture and RWC gave better results than soil matrix potential. There were only slight differences between the adjustments, calculated by using moisture values of the day of measurement or by using mean values over 2, 3, 4 and 5 days before the measurement day. Nevertheless, whatever the model considered, the best results corresponded to those calculated with the moisture value of the measurement day.

As the ‘Expo’ model gave the best fits, we assessed the temperature sensitivity for respiration taking the partial temperature derivative of equation 5 that is:

$$\frac{\partial R}{\partial T} = \frac{1}{10}(bf(\theta) + c)R \quad (6)$$

leading to

$$\frac{\partial R}{R} = \frac{1}{10}(bf(\theta) + c)\partial T = g(\theta)\partial T. \quad (7)$$

The temperature sensitivity of respiration $g(\theta)$ is a linear function of soil water (Fig. 4). Using the parameter estimates (Tab. I), it was therefore possible to compare the responsiveness of soil and ecosystem respiration to temperature at different soil water conditions. The slope of the $g(\theta)$ function, b , was 1.417 and 0.467 for soil and ecosystem respectively. At low RWC (0.4), an increase of 1 °C provokes an increase of soil respiration of 5.7% and an increase of ecosystem respiration of 8.6%. For nonlimiting soil water conditions, at $RWC = 1$, the increases of respiration caused by a 1 °C temperature increase are of 8.5% and 16.5% for soil and ecosystem respectively.

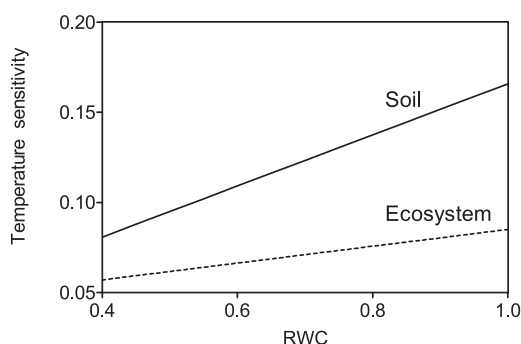


Figure 4. Dependency of temperature sensitivity of respiration on relative water content (RWC). The solid line corresponds to soil respiration and the dotted line to ecosystem respiration.

4. DISCUSSION

Soil CO₂ efflux and soil moisture of the dry plots experienced small variations over the year highlighting the importance of the control by soil water. Relative soil water content remained quite constant around 0.5 (Fig. 1a), that is a soil matrix potential lower than -1 MPa. Bacterial respiration is severely restricted below -1.5 MPa, whereas root and saprophytic fungi respiration is less affected. Fungi respiration remains quite constant till -2 MPa [31, 50]. Coarse root respiration is not affected by our treatment as the volume of soil submitted to water stress imposed in the experimental plot is much smaller than the volume of soil exploited by these roots. The water manipulation treatments done in Puéchabon combine the seasonal short-term variations of soil moisture (Control) with long-term imposed soil moisture (D and W treatments). Due to the small size of the plots (0.09 m²), we could assume that the treatments had no effect on coarse root respiration. On the contrary, long-term effects on microbial biomass composition and activities could be eventually provoked by the water manipulation. The differences in soil respiration for the August and September measurement (Fig. 1a) when temperature and RWC were quite comparable could be possibly due to such an effect. Acclimation of microbial populations to long-term modifications of soil water status should be tested on controlled experiments to identify some possible mechanisms of regulation.

A large body of literature considers soil temperature and water content as two of the most important parameters controlling the variations of soil respiration [14, 24, 34, 41]. The strong seasonal variations of soil CO₂ efflux recorded in our study re-emphasize these controls by temperature and soil moisture as mentioned in previous studies in Mediterranean [4, 10, 12, 15, 32, 38] or semi-arid conditions [17]. When soil water content remains constantly high, temperature is the only parameter related to soil respiration variations [28, 30, 46, 47]. In the majority of the studies, soil moisture plays an important role and many functions have been proposed to describe it [11, 49]. Interactions between both factors are emphasized by [18], but only few models consider them [6, 17]. Carlyle and Ba Than [9] have shown that the Q_{10} factor of respiration varies with soil moisture. The model 'Expo' based on the assumption that the temperature effect was dependent on soil moisture

gave the best fit in our case and could be proposed as a generic model when strong seasonality of the rainfall regime and consequently soil moisture conditions is the rule, as in the Mediterranean climate. The temperature sensitivity of soil respiration was strongly affected by soil water status (Fig. 4) leading to severe limitations under low RWC values. Expressing the moisture as RWC over the five days preceding the measurement day gave slightly better results than expressing it as soil matrix potential. The matrix potential theoretically allows to compare soils of different texture, but there is no general agreement in the literature concerning the best way to describe the effect of soil moisture on microbial processes [40]. In our case, it could be noted that the main differences between the models using RWC or matrix potential were observed in the period of drying event after rainfall.

Strong limitations of ecosystem respiration caused by soil drought were recorded during the four years of measurements. The same pattern was observed too in other Mediterranean evergreen *Q. ilex* forests in Italy [37]. The temperature sensitivity of ecosystem respiration was less severely affected by soil water status than soil respiration. The distinct time-scales of responses between microbial population and perennial ligneous plants have to be considered among the several possible mechanisms accounting for this distinct control. For instance, in the Puéchabon conditions we observed that a small summer rain of 5 mm rewetting the superficial soil layer provoked a strong flush of soil respiration though not having significant effect on plant gas exchanges.

The dependence of ecosystem respiration on soil temperature and moisture provoked important embedded fluctuations at daily and seasonal scales. Over the four years of study, soil temperature was always < 10 °C from the beginning of November to mid-March. During these periods, respiration was not affected by severe soil moisture limitations. In contrast, when soil temperature was higher than 10 °C, i.e. 240 days per year, respiration was severely depressed when RWC was under 0.7. Over the four years, these environmental conditions occurred on 86 days, i.e. 36% of the high soil temperature periods. The year 1998 was the driest with 40% of the non-temperature limited period affected by soil moisture limitations. This value was only 31% in 1999 and 37% in 2000 and 2001. As for the soil, ecosystem respiration models cannot reproduce the strong variations of daily measurements by a simple multiplicative effect of soil moisture and temperature. In contrast, this behaviour is adequately described ($r^2 = 0.79$, RMSE = 0.54) by the 'Expo' model where temperature sensitivity is under soil moisture control.

Soil and ecosystem respirations are under the control of both temperature and soil moisture, but these two variables are not independent, the effects of temperature being affected by the soil moisture level. The temperature sensitivity of respiration was strongly dependent of soil water status for both soil and ecosystem. Interestingly, the sensitivity is much higher for soil than for ecosystem. This results in large uncertainties to predict how the carbon storage could be affected by climatic changes. Despite their complexity, studies dealing with the parameters controlling respiration are necessary, respiration being the key factor of the ecosystem carbon balance in Europe [48]. It has been shown that the increase of temperature has a greater impact on the global respiration of the ecosystem

than on primary production [24]. The higher control by topsoil moisture and higher temperature sensitivity for soil respiration than for ecosystem respiration shown in the Puéchabon forest should be confirmed for other water-limited ecosystems.

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