Ecosystem respiration in two Mediterranean evergreen Holm Oak forests: drought effects and decomposition dynamics

M. REICHSTEIN*†, J. D. TENHUNEN*, O. ROUPSARD‡, J.-M. OURCIVAL‡, S. RAMBAL‡, S. DORE§ and R. VALENTINI§

Department of Plant Ecology, University of Bayreuth, D-95440 Bayreuth, Germany, ‡DREAM Unit, Centre d'Ecologie Fonctionelle et Evolutive, CNRS (1919) route de Mende, Montpellier, France, and §Department of Forest Science and Environment, University of Tuscia, 01100 Viterbo, Italy

Summary

1. We present ecosystem respiration data from two Mediterranean forest sites in central Italy (Castelporziano) and southern France (Puéchabon) in order to analyse the role of soil drought and decomposition dynamics using different models.

2. Ecosystem respiration was derived from continuous eddy covariance measurements. The entire data set was separated into 5-day periods. For each period a function depending on three parameters was fitted to the scatter of eddy CO_2 flux versus photosynthetic photon flux density. The y intercept of each curve was taken as an estimate of the average night-time ecosystem respiration during the period. The ecosystem respiration was analysed with different regression models as a function of soil water content and temperature.

3. Ecosystem respiration ranged from 1 to 7 $\mu mol\ m^{-2}\ s^{-1}$ and showed a clear seasonality, with low rates during drought periods and in winter. The regression model analysis revealed that in drier soil, ecosystem respiration was more sensitive to soil moisture than is expressed by the often used hyperbolic model.

4. In contradiction to a simple multiplicative model, the Q_{10} of ecosystem respiration was not independent of moisture, but increased from nearly 1·0 at low moisture to above 2·0 at field capacity. Several explanations are discussed.

5. Of the variance in ecosystem respiration, 70–80% was explained with a model where Q_{10} of ecosystem respiration is a function of soil water content.

6. For the Puéchabon site, a soil carbon-balance model predicted only small changes in litter pool size (max. 7%), which caused only minor changes in soil microbial respiration (0·1 $\mu mol\ m^{-2}\ s^{-1}$). In contrast, the contribution of microbial regrowth dynamics to ecosystem respiration is estimated to be substantial ($\approx$1·6 $\mu mol\ m^{-2}\ s^{-1}$). The model predicted that soil microbial respiration probably provides the largest contribution to ecosystem respiration ($\approx$50%). The importance of below-ground processes for ecosystem C balances is thus emphasized.

Key-words: Carbon cycle, drought effects, eddy covariance, modelling, temperature effects, Q_{10} value

Functional Ecology (2002) **16**, 27–39

Introduction

To predict long-term trends in carbon sequestration by ecosystems, it is necessary to understand the responses of ecosystem respiration – defined as the sum of soil microbial, root, leaf and stem respiration – to environmental factors (Johnson *et al.* 1996; Jones *et al.* 2000; Valentini *et al.* 2000; Vourlitis & Oechel 1999).

A consensus exists with respect to the importance of temperature and water availability in determining ecosystem CO_2 emissions. Several reviews have examined the analysis and description of temperature induced increases in soil respiration (Kätterer *et al.* 1998; Kirschbaum 1995; Lloyd & Taylor 1994). Less consistent results have been recorded with respect to the influence of soil moisture on respiration, so that different functions describing the dependence have been applied: linear (Epron *et al.* 1999; Norman *et al.* 1992); exponential (Davidson *et al.* 1998; Fang & Moncrieff

†Author to whom correspondence should be addressed. E-mail: markus.reichstein@uni-bayreuth.de

1999; Keith *et al*. 1997); and hyperbolic (Bunnell *et al*. 1977; Carlyle & BaThan 1988; Hanson *et al*. 1993; Schlentner & van Cleve 1985). When describing temperature and moisture effects on soil or ecosystem respiration simultaneously, for example in models of global change, it has been assumed that the effects of individual factors may be multiplicative (Bunnell *et al*. 1977; Fang & Moncrieff 1999; Hanson *et al*. 1993). However, this assumption is not well tested and might lead to an overestimation of the respiration response to warming under dry soil conditions (Borken *et al*. 1999).

Information on the processes controlling net C gain have often been obtained in extreme habitats, e.g. shaded, hot or cold. The Mediterranean environment is special in that prolonged drought re-occurs annually in a relatively predictable, simple manner (long-term slow drying of the system followed by re-wetting). Thus Mediterranean sites are ideal to examine temporal changes in ecosystem C balance (CO_2 fixation, leaf and root phenology, litter and microbial dynamics) in response to soil water availability and temperature (Bottner *et al*. 1995; di Castri 1981; Rovira & Vallejo 1997).

While several studies of soil respiration in Mediterranean regions have been conducted in the laboratory (Leirós *et al*. 1999) and with small chambers in the field (Casals *et al*. 2000; Merzouki 1986; Pinol *et al*. 1995), eddy covariance non-intrusively estimates C fluxes under field conditions and at the stand level (Baldocchi *et al*. 1996). Here we report hourly net ecosystem CO_2 exchange measured using eddy covariance in two Mediterranean *Quercus ilex* L. forests. We attempt to estimate the seasonal course of ecosystem respiration. Our major objective was to evaluate cur-rent model assumptions describing soil respiration as a function of soil temperature and moisture. Further, by using a C balance model, the contribution of soil microbial respiration to total ecosystem respiration was estimated. How variation in soil litter pools may contribute to variability in overall ecosystem CO_2 losses was also tested.

Materials and methods

SITE DESCRIPTION

An overview over the site characteristics is given in Table 1. Although climatically quite similar, the two sites differ substantially with respect to water availability due to pedological conditions. Owing to the low maximum soil water availability (150 mm) at Puéchabon/France, this site is more xeric than the Castelporziano/Italy site, where roots have access to groundwater (Valentini *et al*. 1992). These conditions are the main reason for the weaker canopy development at Puéchabon (Table 1). See Manes *et al*. (1997); Merzouki (1986); Joffre *et al*. (1996) for a more extensive description of the site.

DATA COLLECTION AND TREATMENT

Net ecosystem CO_2 exchange was measured continuously by eddy covariance (Baldocchi *et al*. 1996). The instruments were a 3D sonic anemometer (Solent, Gill Instruments Ltd, Lymington, UK) which measures the wind vector and air temperature, and a closed-path infrared gas analyser sampling with 10 Hz (IRGA; LI6262, Li-Cor Inc., Lincoln, NK, USA). The eddy

Table 1. Characteristics and data collection at the study sites Puéchabon and Castelporziano

	Puéchabon	Castelporziano
Characteristics		
Location and terrain	France, flat plateau (43·75°N, 3·6°W, 250 m a.s.l.)	Italy, flat basin (41·7°N, 12·3°E, 7 m a.s.l.)
Annual mean temperature (°C)	13·4	15·5
Annual precipitation (mm)	812	740
Canopy species, cover (%)	*Quercus ilex* L. (>90) *Quercus pubescens* L. (<10)	*Quercus ilex* L. (>90) *Quercus suber* L. (<10)
Leaf area index ($m^2 m^{-2}$)	2·9	3·5
Stand height (m)	6	10
Soil texture	clay loam, >70 vol% coarse fraction (>2 mm)	sand, <5 vol% coarse fraction
Soil parent material	Jurrasic limestone	Aeolic sands
Management history	coppice, last cut shortly after 1945	unmanaged for centuries
Data collection		
Flux measurements	Eddy covariance system at 13 m, sap flow with Granier-type sensor at 12 trees	Eddy covariance system at 15 m, sap flow with Granier-type sensors at three trees
Soil conditions	Neutron probe at six locations and from 0 to 450 cm depth	TDR at five locations in depths 0–20, 30–50, 70–90 cm, soil temperature at 10 cm, three locations
Meteorological variables	Above the canopy: air temperature, global and net radiation and H_2O pressure, wind speed: all at 13 m	above the canopy: air temperature, global and net radiation and H_2O pressure at 16·5 m, wind speed at 12·5 m

covariance system and data processing were as described by Aubinet *et al.* (2000) (see Table 1 for further information). The half-hourly data sets of CO_2 exchange (Fc) and meteorological conditions were aggregated to hourly data by averaging the two observations per hour. In a preparatory step, night-time CO_2 fluxes at air temperatures between 10 and 15 °C and with apparently high soil moisture were plotted against friction velocity ($u*$). At both sites, these fluxes increased with $u*$ at low $u*$, and saturated at higher friction velocities. Based on a fitted function, $Fc(u*) = Fc_{max} [1 - \exp(-k\,u*)]$, at least 95% of the maximal night-time CO_2 flux was reached at friction velocities above 0·2 m s^{-1} (k always >15 s m^{-1}). All eddy covariance data with $u* < 0.2$ m s^{-1} were excluded from the analysis, as it is likely that under these conditions storage and advection can reduce gas fluxes through the boundary layer. Similarly, negative night fluxes (i.e. with night C uptake) were excluded. In total, 2260 values or 47% of the Puéchabon, and 4432 values or 60% of the Castelporziano hourly data were excluded.

Ecosystem respiration was estimated from scatterplots of net ecosystem CO_2 exchange (NEE) versus photon flux density over the canopy as follows. The time-series data were separated into periods of 5 days starting at January 1. For each period with more than 10 night-time observations, the three-parameter stepwise linear regression model:

$$F_c = \max(-\alpha \cdot PPFD; -F_{c,sat}) + R_{eco} \qquad \text{eqn 1}$$

was fitted to the observed hourly eddy covariance flux data ($F_{c,obs}$) (modified Levenberg–Marquardt algorithm, Visual Numerics Inc., 1993) where $PPFD$ is the photosynthetic photon flux density (µmol m^{-2} s^{-1}), α is the apparent ecosystem quantum-use efficiency (µmol C m^{-2} s^{-1} µmol photons m^{-2} s^{-1}), Fc_{sat} is the gross C uptake at saturating light (µmol C m^{-2} s^{-1}), and R_{eco} is the ecosystem respiration (µmol m^{-2} s^{-1}). In addition, for each 5-day period the averages of air and soil temperature, friction velocity ($u*$) and soil water content (SWC) were computed, excluding the same data as in the regression analysis. This procedure resulted in a data set of 5-day means of air and soil temperatures, SWC, $u*$ and R_{eco}. For 86% (Puéchabon) and 58% (Castelporziano) of the 5-day periods, respectively, it was possible to provide an estimate of ecosystem respiration according to this procedure.

The SWC was measured bi-weekly at Castelporziano by time domain reflectometry, and monthly at Puéchabon with neutron probes (cf. Table 1). To interpolate the discontinuous measurements of SWC, a mechanistic model of one-dimensional soil heat and water was utilized (Moldrup *et al.* 1989; Moldrup *et al.* 1991, slightly modified as in Reichstein 2001). Driven by hourly observations of global radiation, air temperature, precipitation, vapour pressure deficit and wind speed, this model simulates infiltration and evaporation of water into/from the soil, unsaturated water flow (Richards equation) and extraction of soil water by roots. The total demand of water for transpiration was given by observations of sap flow, which have been performed continuously at both sites. Soil temperature was measured continuously at 10 and 30 cm depth at the Castelporziano site, and was used to test the soil heat transport model. At the Puéchabon site, soil temperatures were generated only by the model.

ECOSYSTEM RESPIRATION MODELS

The ecosystem respiration data were analysed with four different models, each with different and partly mutually exclusive assumptions. In all models, soil temperature and soil moisture in the upper soil layer were taken as predictors of ecosystem respiration.

In the first two models, ecosystem respiration was described as being multiplicatively dependent on soil temperature (T_{soil}) and soil water content (SWC):

$$R_{eco} = R_{eco,ref} \cdot f(T_{soil}) \cdot g(\text{SWC}) \qquad \text{eqn 2}$$

where $R_{eco,ref}$ is the ecosystem respiration at 15 °C and optimal soil moisture, and $f(T_{soil})$ is the function of Lloyd & Taylor (1994), normalized to 15 °C:

$$f(T_{soil}) = e^{E_0\left(\frac{1}{T_{ref} - T_0} - \frac{1}{T_{soil} - T_0}\right)} \qquad \text{eqn 3}$$

where T_{ref} and T_0 are fixed to 15 and –46 °C, respectively. E_0, in contrast, was considered to be a free parameter and was fitted to each data set.

Models I and II differ only in the moisture functions used. While in model I the commonly applied saturation function

$$g(\text{SWC}) = \frac{SWC}{SWC_{1/2} + SWC} \qquad \text{eqn 4}$$

(cf. Bunnell *et al.* 1977; Hanson *et al.* 1993) was used, in model II a new function

$$g(SWC) = \frac{SWC - SWC_0}{(SWC_{1/2} - SWC_0) + (SWC - SWC_0)}$$

$$\text{eqn 5}$$

was used. This is a generalization of model I and allows higher sensitivity of respiration to soil water content during dry periods. The parameters $SWC_{1/2}$ and SWC_0 are the soil water content at which the half-maximal respiration occurs and the residual soil water content at which respiration is zero, respectively. SWC can be expressed either in absolute terms, as m^3 water per m^3 total soil volume (θ), or as relative soil water content ($RSWC$) as a fraction of field capacity: $RSWC = \theta / \theta_{\text{at field capacity}}$ (field capacity operationally defined as SWC at a matric potential of 330 hPa).

Models I and II imply that the temperature sensitivity of ecosystem respiration is independent of soil moisture. This assumption is challenged by model approaches III and IV. In model III the data set was

split into soil moisture classes (of equal number of observations), and for each class the temperature dependence of ecosystem respiration was described by a simple Q_{10} function:

$$f(T_{soil}) = Q_{10}^{\frac{T_{soil} - T_{ref}}{10}}$$ eqn 6

($T_{ref} = 15\ °C$). For each moisture class an independent estimate of Q_{10} was obtained. In model IV, the Q_{10} of ecosystem respiration was explicitly linearly dependent on SWC:

$$f(T_{soil}) = Q_{10}(SWC)^{\frac{T_{soil} - T_{ref}}{10}} \text{ with } Q_{10}(SWC)$$
$$= b_1 + b_2 \cdot SWC$$ eqn 7

A positive b_2 would mean, for example, that temperature sensitivity increases with increasing SWC, in contrast to the assumption that temperature and moisture act multiplicatively on ecosystem respiration. Parameters of all models were estimated from the data sets of 5-daily aggregated ecosystem respiration, soil temperature and soil moisture.

SOIL MICROBIAL RESPIRATION FROM DECOMPOSITION

We tested if varying litter pools can contribute substantially to the seasonality of respiration. The introductory C balance model (ICBM, Andrén & Kätterer 1997) was used, which assumes two organic C fractions (C_Y: young, labile; C_O: old, stable, kg m^{-2}) decomposed by first-order kinetics [rate constants k_1, k_2 (year^{-1})]. A fraction h of the outflow from C_Y is transformed into C_O (h represents humification), while the old C fraction is entirely decomposed to CO_2. Litter input i enters the system through the labile C pool (C_Y):

$$\frac{d}{dt} C_Y(t) = i - r \cdot k_1 \cdot C_Y(t)$$ eqn 8

$$\frac{d}{dt} C_o(t) = r \cdot h \cdot k_1 \cdot C_Y(t) - r \cdot k_2 \cdot C_o(t)$$ eqn 9

For each time step, the inputs to the ICBM are litter fall (kg m^{-2} per unit time) and abiotic conditions for decomposition expressed as a scalar r. The annual leaf-litter fall had been measured at the site for 10 consecutive years (Joffre *et al.* 1996), while the intra-annual dynamics of leaf-litter fall and the ratio of total litter to leaf litter were assumed to be equal to a nearby site (Lossaint & Rapp 1978). The scalar r was computed hourly with the functions of model IV (Eqns 5 and 6).

For the parameterization of the ICBM, the mass of litter per m^2 (interpreted as C_Y) was measured in the field by sampling the litter from 30 randomly selected circles of 20 cm diameter at Puéchabon in February 1999. For the estimation of area-based soil C storage, reliable estimates of the soil C mass per kg soil were available at Puéchabon. For converting these into area-based values, the bulk density and the stone content of the soil were estimated in the field as in Deutschmann *et al.* (1994). The rate constant k_1 and the humification coefficient h were estimated from decomposition experiments of *Q. ilex* litter (leaves and flowers; Gillon *et al.* 1994) according to Andrén & Kätterer (1997). The decomposition rate constant k_2 was parameterized by solving the steady-state equation (eqn 9) for k_2 (cf. Andrén & Kätterer 1997; Reichstein *et al.* 2000), where the subscripts tot and avg mean total and average:

$$C_{tot,steady-state} = \frac{i_{avg} \cdot (1/k_1 + h/k_2)}{r_{avg}}$$ eqn 10

While the steady-state assumption is not proven (potentially introducing errors into the calculation of k_2), small errors in the stable C decay constant k_2 do not alter the short-term dynamics. The independent calibration of the soil organic C balance model (ICBM) for the Puéchabon site leads to the parameterization given in Table 2 and the time-course of litter input as shown in Fig. 1. The litter input rate has a distinct maximum in May and a secondary maximum in November.
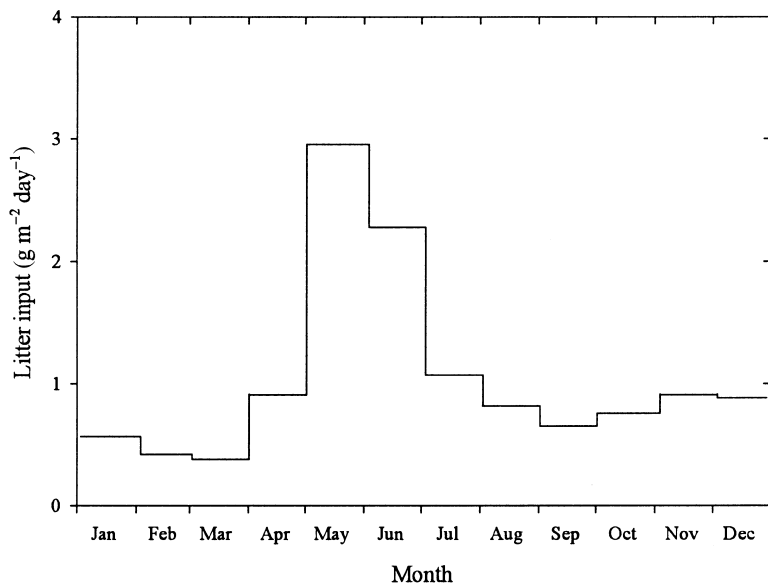
STATISTICAL ANALYSIS

Standard errors of non-linear regression parameters were estimated by a bootstrapping algorithm. The original data sets consisting of 5-day aggregated ecosystem respiration, soil temperature and SWC were randomly resampled (with replacement) 500 times, where each resample was made up to the same number of data points as the original data set. The non-linear regression (*nonlinregress* in PV-WAVE 6; Visual Numerics Inc 1993) was run for each resample, resulting in 500 parameter estimates per original data set. The standard deviation of these 500 estimates is a good measure of the random error associated with the individual regression parameters (Efron & Tibshirani 1993).

Model performance was measured with the statistic 'modelling efficiency' (MEF) as recommended by Janssen & Heuberger (1995), defined as

$$MEF = 1 - \frac{\sum_{i=1}^{N}(OBS_i - SIM_i)^2}{\sum_{i=1}^{N}(OBS_i - \overline{OBS})^2}$$ eqn 11

where OBS_i and SIM_i are the corresponding observed and simulated values. In contrast to the coefficient of determination (r^2), the modelling efficiency measures not only the correlation between modelled and observed data, but also their 'coincidence', i.e. the deviation from the 1 : 1 line.

Table 2. Parameterization of the introductory C balance model (ICBM) for the Puéchabon site

Parameter	Value
Total C stock C_{tot} (kg C m^{-2})	3·25
Labile C stock C_Y (kg C m^{-2})	0·38
Annual litter input I (kg C m^{-2} year^{-1})	0·384, see Fig. 1 for time-course
Decomposition rate coefficients k_1; k_2 (year^{-1})	0·51; 0·03
Humification coefficient h (fraction)	0·20

Fig. 1. Estimated annual course of litter C input (above- and below-ground) for the Puéchabon site.

Results

SOIL TEMPERATURE AND WATER DYNAMICS

During the study years, both sites experienced characteristic Mediterranean weather conditions (Fig. 2). The drought at Puéchabon lasted for slightly more than 2 months (from the end of June j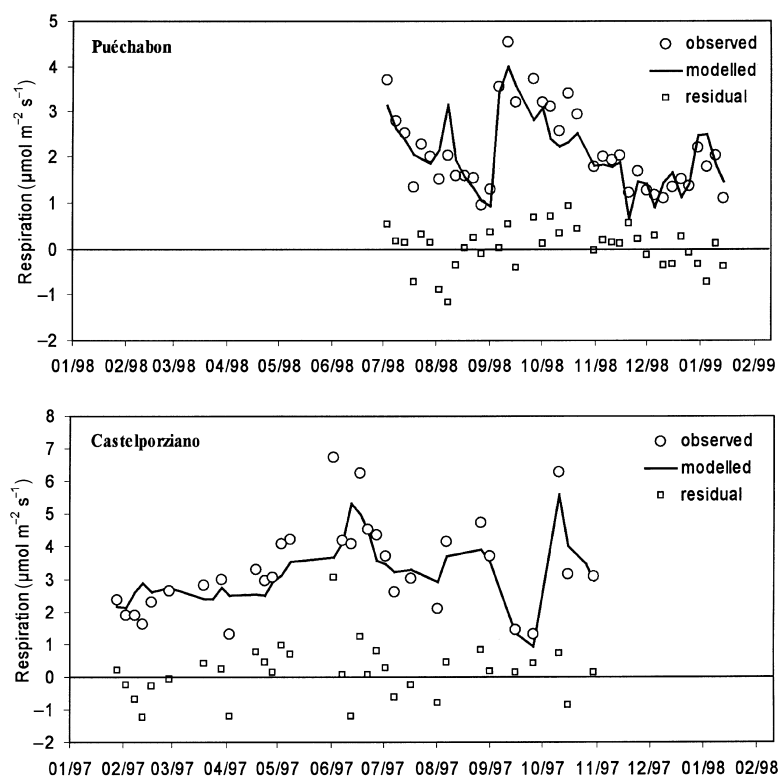ust before the measurements started until the beginning of September). Soil water was severely depleted during this period. Low rainfall during August 1998 recharged only the upper centimetres of the soil (Fig. 2, top), while intensive autumn rainfalls in September rapidly and completely recharged the soil. Soil temperature fluctuated between 20 and 30 °C during the summer drought and declined to near zero in winter (Fig. 2, bottom). At Castelporziano, the summer drought lasted from the beginning of June until October, leading to a continuous soil water depletion. Similar to Puéchabon, temperatures at Castelporziano were highest in July and August, but were slightly lower than at Puéchabon. At both sites, water dynamics in the upper soil layer were well described by the model (Fig. 2, top). At Puéchabon and Castelporziano, modelling efficiencies were 0·64 and 0·96, mean absolute errors 0·004 and 0·016 m^3 m^{-3}, respectively. Daily averages of modelled soil temperatures compared well to the observed data at the Castelporziano site (Fig. 2, bottom, MEF > 0·9).

ECOSYSTEM RESPIRATION

The annual course of ecosystem respiration was similar at both sites, exhibiting a clear decrease from early to late summer, and an immediate strong increase after the first rain in autumn (Fig. 3). However, the absolute rates (calculated for 15 °C and optimum water content) differed between the sites (Table 3), and their ratio approximated the leaf-area ratio between the sites (Table 1).
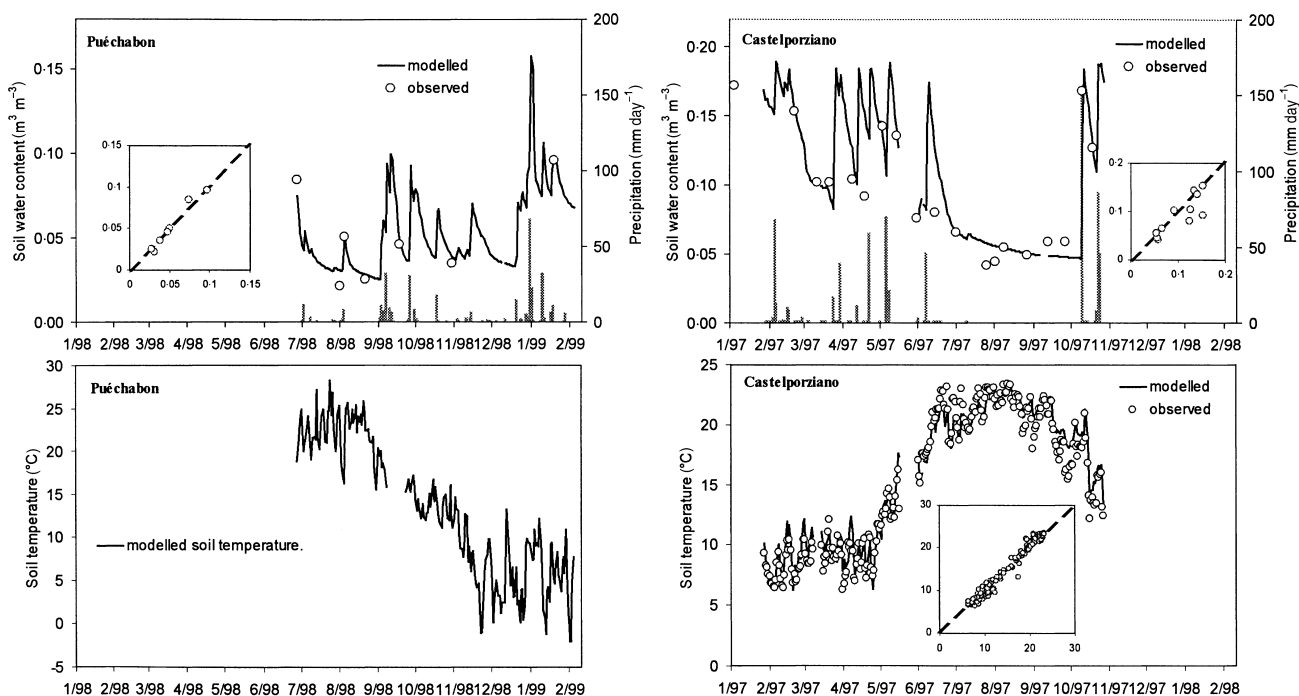
Fig. 2. Upper panels, daily precipitation (grey bars), and modelled and observed upper-layer soil-water dynamics for the Puéchabon and Castelporziano sites. Insets represent scatter plots of modeled versus observed soil-water content in 0–20 cm (m^3 m^{-3}). Lower panels, time-course of modelled daily average soil temperatures at 10 cm depth at the Puéchabon and Castelporziano sites. Also shown are observed soil temperatures, which were only available at the Castelporziano site at 10 cm depth. The inset shows the observed versus modelled soil temperature at the Castelporziano site.

Fig. 3. Seasonal course of 5-day averages of ecosystem respiration at the Puéchabon and Castelporziano sites, derived from eddy covariance measurements, modelled by non-linear regression with model IV, and residual.

the residual plot versus soil moisture (Fig. 4a) it is obvious that the model had a systematic bias, underestimating the flux at medium water contents and overestimating the flux at high and low water contents. Additionally, this model gave unrealistic results at high water contents (Fig. 4b): according to this model there was an increasing flux with increasing moisture, even above field capacity.

In contrast, the modified soil moisture function (model II) did not exhibit these properties (Fig. 4b). The shape of the difference curve is quite similar to the residual curve in Fig. 4. The modified soil moisture function (model II) provides distinctly better fits (Table 4), modelling efficiency and r^2 ranging between 0·68 and 0·83. Also, model II was unbiased for moisture and temperature (see residual plots, Fig. 5). The residuals were statistically independent from friction velocity (u^*) (Fig. 5), suggesting that the removal of u^* below the threshold value was satisfactory. Finally, with the optimized parameters the shape of the curve was more realistic than with model I (Fig. 4b; Table 3): it rapidly approached a maximum and increased little in wet soil. On both sites, the model fit resulted in a parameterization with a high sensitivity of ecosystem respiration to soil moisture. The half-maximal water content ($\theta_{1/2}$) was less than 3% above the residual water content.

Although model II satisfactorily described the response to drought without bias, one assumption can be questioned from the results of model III and IV: the assumption that temperature sensitivity (Q_{10}) is independent of soil moisture. In model III the data were classified into moisture classes, and Q_{10} functions fitted to the data (Fig. 6). Respiration at a reference temperature of 15 °C increased with increasing moisture

The different non-linear regression models of ecosystem respiration performed quite differently (Table 3). The widely used model I explains only 70% of the variance of ecosystem respiration for the Puéchabon site and 54% for Castelporziano. More importantly, from

Table 3. Non-linear regression results of ecosystem respiration versus soil temperature and soil water content with models I and II. Approimate standard errors of the parameter estimates are shown in parentheses. Reference temperature for R_{eco} is 15 °C

Model parameters:	Unit	Puéchabon		Castelporziano	
		Model I	Model II	Model I	Model II
$R_{eco,ref}$	µmol m^{-2} s^{-1}	8·79 (3·30)	3·91 (0·36)	9·54 (4·54)	4·54 (0·47)
E_0	1/K	185 (24·9)	200 (18·9)	272 (49·2)	263 (39·3)
T_0 (*fixed*)	°C	−46·02	−46·02	−46·02	−46·02
corresponding Q_{10} at 5 °C	–	2·05	2·18	2·90	2·79
15 °C	–	1·65	1·74	2·10	2·04
25 °C	–	1·45	1·49	1·72	1·69
	m^3 m^{-3}	0·143 (0·075)	0·037 (0·0039)	0·221 (0·166)	0·063 (0·0076)
SWC$_{1/2}$	% of FC#	159 (84)	41·6 (3·97)	158 (118)	45·0 (5·40)
	m^3 m^{-3}	n.a.§	0·024 (0·0014)	n.a.	0·044 (0·0031)
SWC$_0$	% of FC	n.a.	26·5 (1·62)	n.a.	31·8 (2·20)
Model statistics:	–				
Mean absolute error	µmol m^{-2} s^{-1}	0·38	0·26	0·71	0·57
Ratio of scatter	–	1·54	1·20	2·03	1·41
Root mean squared error (RMSE)	µmol m^{-2} s^{-1}/ % of mean	0·49/23·1%	0·37/17·3%	0·84/26·5%	0·69/21·8%
Modelling efficiency	–	0·70	0·83	0·54	0·68
r^2	–	0·70	0·83	0·54	0·68

#: FC = field capacity; §: n.a. = not applicable.
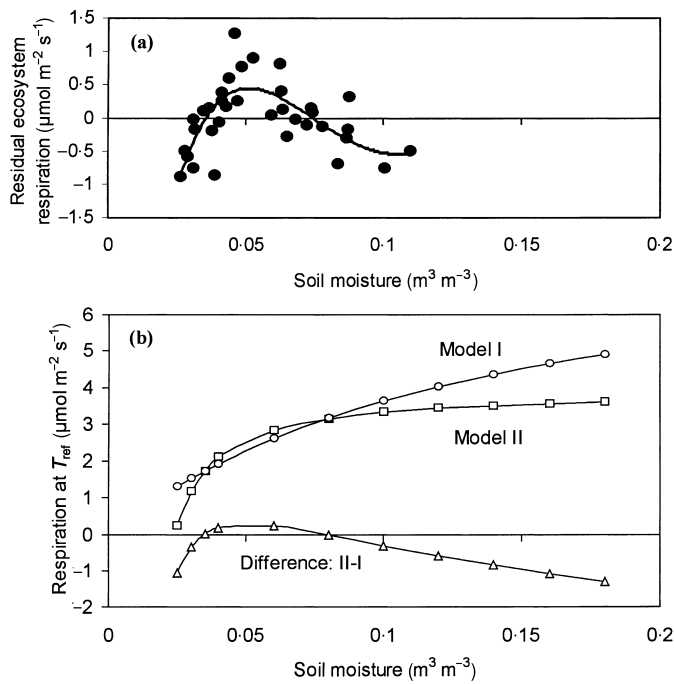
Fig. 4. (a) Residual plot of ecosystem respiration from model I versus soil moisture for the Puéchabon site, showing the model bias. The polynomial relationship of third degree is significant (*F* test, $P < 0.05$). (b) Comparison between ecosystem respiration as predicted by models I model II for the Puéchabon site.

(Fig. 7). In addition, the Q_{10} of respiration at both sites increased monotonically from about 1·0 (no response) in dry soil to above 2·0 at field capacity (Fig. 7). When data from the two sites were pooled, the trend of increasing Q_{10} with soil water content was highly significant ($P < 0.01$; $N = 7$; Spearman's rank correlation). A moisture-dependent Q_{10} was also found when the Q_{10} was expressed as a linear function of soil moisture (model IV, eqn 6): At both sites the slope was pos-

itive, and for Puéchabon the Q_{10} of respiration increased by 0·96 if soil water content increased by 0·1 m³ m⁻³ (Table 4). However, in this multiple non-linear regression the standard errors were relatively large. Although the fit of model IV was good (Fig. 8a), the time-course of the residuals varied seasonally (Fig. 3), for example, at the Puéchabon site a trend in the residuals was perceptible from August to October.

MODELLED SOIL MICROBIAL RESPIRATION

The estimated soil microbial respiration with ICBM averaged 1·0 µmol m⁻² s⁻¹ or about 50% of the estimated ecosystem respiration in the period. The relative proportion of soil microbial respiration to ecosystem respiration did not change substantially over time, despite the non-uniform litter input. According to the ICBM, the labile C pool changed by a maximum of 4·4 mol m⁻² (7%) and normalized soil microbial respiration changed by an even smaller percentage (Fig. 9). The most rapid change of approximately –2% per month occurred in September and October.

Discussion

The normalized ecosystem respiration rates of the two sites ($R_{eco,ref}$) differed between the sites by a factor of 1·16, nearly the same factor as the leaf area index (LAI; 1·21). This result is expected, as leaves themselves respire, and supporting respiring tissue (stems, roots) and litter input to the soil generally increase with LAI. If species composition and other conditions do not change, LAI should be a good predictor of normalized ecosystem respiration. If this hypothesis remains valid, it could profitably be used in combination with remotely sensed vegetation indices.

Table 4. Non-linear regression results of ecosystem respiration versus soil temperature and soil water content with models III and IV. Approximate standard errors of the parameter estimates are shown in parentheses. Reference temperature for R_{eco} is 15 °C

Parameter:	Unit	Puéchabon Model III at moisture Vol-%:				Model IV	Castelporziano Model III at moisture Vol-%:			Model IV
		3·12	4·1	6·3	8·6		6·59	13·0	15·9	
$R_{eco,ref}$	µmol m⁻² s⁻¹	1·47 (0·17)	2·11 (0·24)	2·83 (0·14)	3·01 (0·11)	3·81 (0·37)	2·98 (0·69)	3·74 (0·29)	3·72 (0·33)	4·28 (0·51)
Q_{10}	–	1·26 (0·18)	1·34 (0·32)	1·65 (0·14)	1·98 (0·13)	= 1,14 (0·26) +9·60 (4·28)·θ$	0·93 (0·37)	1·70 (0·31)	2·32 (0·39)	= 1·17 (1·06) + 5·95 (7·22)·θ$
SWC$_{1/2}$	m³ m⁻³ % of FC#	n.a.§	n.a.	n.a.	n.a.	0·037 (0·0037) 40·7 (4·2)	n.a.	n.a.	n.a.	0·057 (0·011) 40·8 (11·9)
SWC$_0$	m³ m⁻³ % of FC	n.a.	n.a.	n.a.	n.a.	0·023 (0·0021) 25·6 (2·34)	n.a.	n.a.	n.a.	0·045 (0·0034) 31·9 (3·73)
Statistics:										
MAE	µmol m⁻² s⁻¹	0·32	0·48	0·30	0·21	0·26	0·93	0·58	0·65	0·56
RMSE	µmol m⁻² s⁻¹	0·41	0·62	0·35	0·25	0·37	1·10	0·69	0·74	0·68
MEF	–	0·29	0·19	0·86	0·94	0·83	0·01	0·58	0·72	0·69
r^2	–	0·29	0·19	0·86	0·94	0·83	0·01	0·58	0·72	0·69

$: θ = soil water content (m³ m⁻³); #: FC = field capacity; §: n.a. = not applicable.
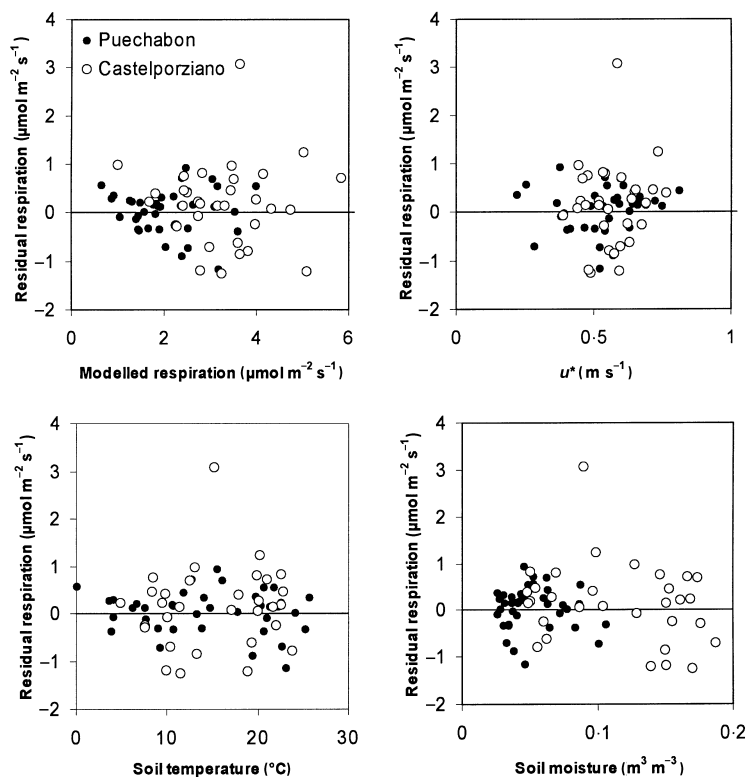
Fig. 5. Residual plots for the non-linear regression of ecosystem respiration dependent on soil moisture and temperature (model II). For both sites, and in all plots, polynomial trends up to the third degree were not significant (F test, $P > 0.05$).
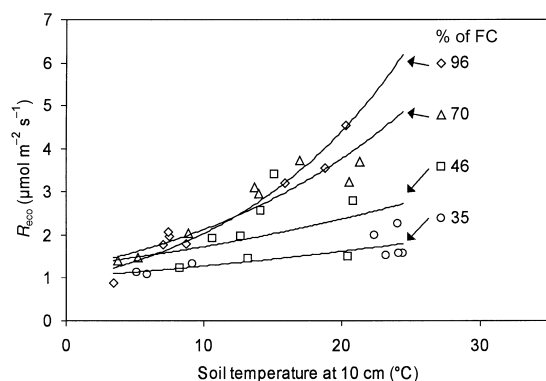

Fig. 6. The relationship between ecosystem respiration (R_{eco}) and soil temperature within four different soil moisture classes at the Puéchabon site. The solid lines represent exponential (Q_{10}) fits for each soil moisture class. For each moisture class, the average soil moisture in percentage of field capacity is indicated beside the symbol.

At both sites ecosystem respiration exhibited a clear seasonality, with maxima occurring in spring and autumn. A clear drop in ecosystem respiration occurs during the drought, and the autumn peak coincided with the first rain event. Consequently, a large proportion of the variance can be explained by a non-linear regression on soil temperature and moisture. The estimated temperature dependence of ecosystem respiration (expressed as Q_{10} at 15 °C) is weaker than previously found for soil C mineralization (Leirós *et al.* 1999), but slightly higher than for leaf respiration (Tenhunen *et al.* 1987) in Mediterranean-type ecosystems.

The residual analysis shows no bias of the temperature function provided by Lloyd & Taylor (1994). However, the often-used simple Michaelis–Menten-type function for the dependence of respiration on soil moisture (e.g. Carlyle & BaThan 1988; Hanson *et al.* 1993) was inadequate to describe the dynamics. It introduces a bias because its sensitivity to soil moisture in dry soil is too low. Thus a modification of this model function is proposed, introducing a residual water content at which respiration ceases (eqn 5). This is consistent with parameterizations based on soil physical retention curves, where the soil water potential is highly sensitive to moisture content in drier soil (Marshall & Holmes 1988) and where a residual water content is often introduced at which water potential converges toward infinity (e.g. van Genuchten 1980). In addition, and in contrast to the 'simple' function, the proposed function (eqn 5) does not predict increasing respiration at water contents above field capacity. The modified function should be preferred for both theoretical and empirical reasons, at least in dry soil.

Inter-site comparisons of parameters such as $SWC_{1/2}$ in this study are difficult, because volumetric soil water content provides no direct indications about water availability. In the highly rocky soil (>70% coarse fraction) at Puéchabon, for example, a water content of $0.06 \text{ m}^3 \text{ m}^{-3}$ indicates a relatively high water availability, while the same volume fraction at Castelporziano represents relatively low water availability. As a surrogate for water availability, the water content can be expressed as a percentage of field capacity, here defined as water content at a matric potential of 330 hPa. Then the $RSWC_{1/2}$ values are quite similar, around 40% of field capacity with overlapping confidence intervals, indicating that relative soil water content is a better measure of soil water availability than absolute volumetric moisture content. It is also possible to use soil water potential as the independent variable in the moisture function, but water potential is not as conveniently measured as volumetric moisture by means of TDR or neutron probe, particularly under very dry conditions.

An assumption made in most soil respiration models is that respiration can be described by a simple multiplicative effect of temperature and moisture. This was challenged for ecosystem respiration by two different data analyses. The temperature sensitivity of respiration was not independent of moisture, but the Q_{10} increased from about 1·0 to >2·0 with increasing moisture, suggesting a model with an increasing Q_{10} for increasing soil moisture (eqn 6). It might be argued that the predictive power of this model IV was similar to model II (only slightly higher r^2), but the relatively good performance of model II results from its 'effective' parameterization via the regression analysis and does not necessarily mean that it is correct. A Q_{10} varying between 0·8 and 2·6 with soil moisture was reported by Carlyle & BaThan (1988). Recently, Borken *et al.* (1999) also found a flatter response
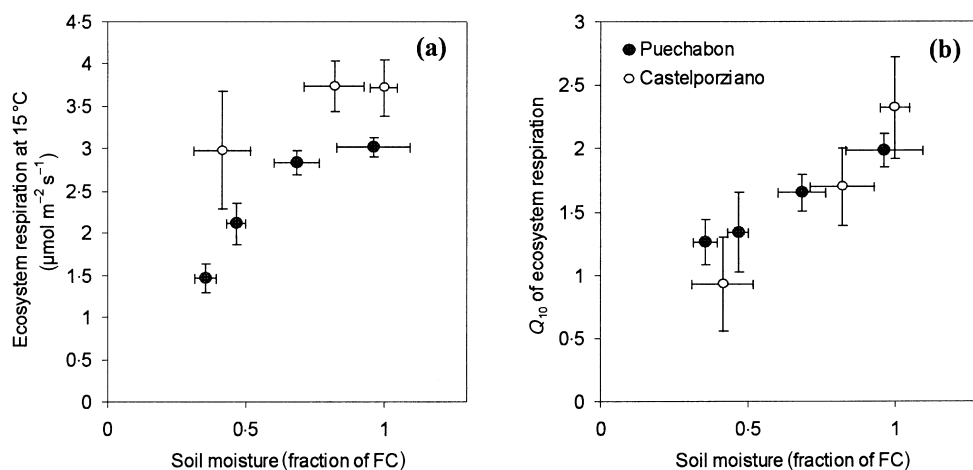
Fig. 7. Results from model III: relationship between (a) ecosystem respiration at $T_{ref} = 15\,°C$ and soil moisture, and between (b) estimated Q_{10} of ecosystem respiration and soil moisture for the Puéchabon and Castelporziano sites. Horizontal error bars represent standard deviation of soil moisture within moisture classes; vertical bars indicate standard errors of estimate for the parameters.
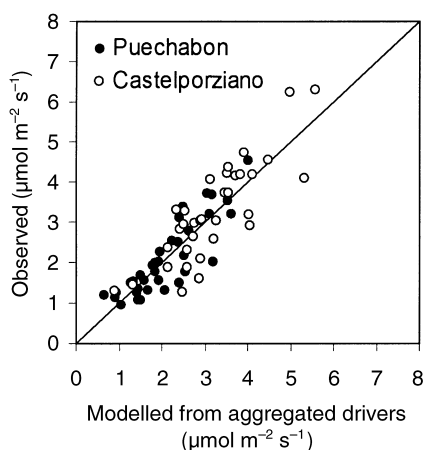
Fig. 8. Scatter plots of observed 5-day mean ecosystem respiration versus regression model IV with 5-day mean drivers.

curve of soil respiration to temperature in an experimental drought plot compared to a well watered plot.

Several mechanisms may account for an apparently variable Q_{10} of soil and ecosystem respiration.

(i) There is evidence that Q_{10} of decomposition is higher for labile than for stable substrates (Anderson 1991; Liski *et al.* 1999). Labile substrates are often associated with coarse fractions (litter), and these dry out first, so that they do not respire under dry conditions. Consequently, the Q_{10} drops, because under dry conditions most respiration comes from more stable material, which only allows a lower Q_{10}.

(ii) A similar effect would occur with partial inactivation of the rhizosphere during soil drying, as a higher Q_{10} was found in the rhizosphere than the bulk soil (Boone *et al.* 1998).

(iii) In the dry period, C assimilation of the canopy was severely reduced, so that fewer assimilates are
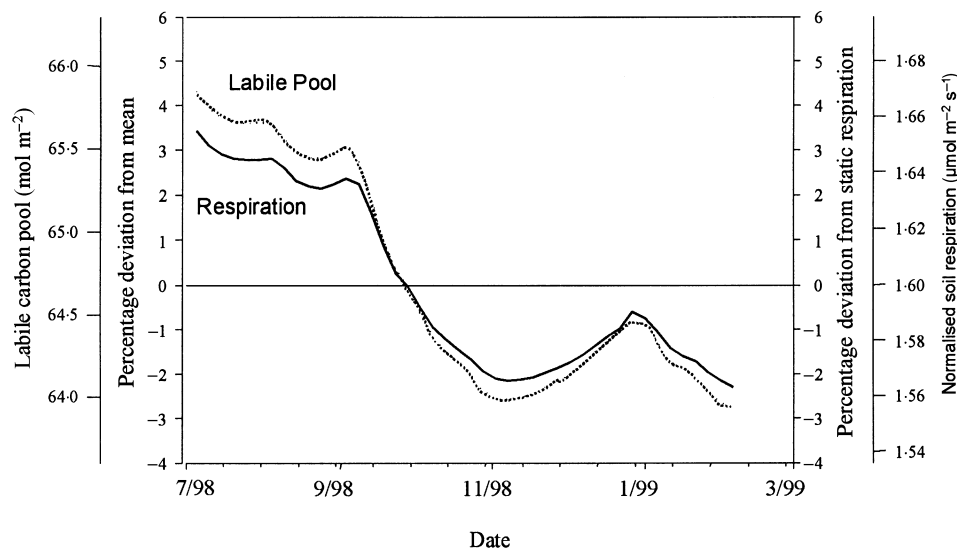
Fig. 9. Development of labile pool size and soil microbial respiration (standardized to 10 °C and to half-maximal moisture), expressed in relative (inner axes) and absolute (outer axes) units for the Puéchabon site. Static respiration means respiration when the labile pool is assumed to be constant, as in the regression model.

expected to be transported towards the rhizosphere (source limitation of rhizosphere respiration) leading to the same effect as in (ii).

Because whole-ecosystem respiration was studied here, we emphasize the importance of effects such as varying Q_{10} at the ecosystem level. We need more information on how temperature and drought affect respiration. These results have implications for future climate-change scenarios (e.g. Cox *et al.* 2000). They stress the importance of changes in soil moisture in two ways: not only is the direct sensitivity of ecosystem respiration to soil moisture in a dry soil important, but also the indirect moisture effect on the temperature dependence would reduce the respiration-enhancing effect of higher temperatures. The results of Lloyd & Taylor (1994), indicating a decreasing Q_{10} of soil respiration with increasing temperature, may result from the correlation between drier and warmer soil temperatures. In support of this idea, Kätterer *et al.* (1998) found no such temperature effect on the Q_{10} from a compilation of laboratory studies which were performed at optimal moisture. This calls for testing of other data sets to determine whether this pattern is general.

With the regression model IV (eqns 5 and 6), more than two-thirds of the variation in measured ecosystem respiration was explained at both sites. The variation not explained by the models may be associated with several errors. At least four factors might have contributed to this partial disagreement.

(i) There is still some random error in the eddy covariance data, despite aggregation into 5-day periods. Particularly when the data were fluctuated around the relatively stable model values (e.g. February to April in Castelporziano, or December in Puéchabon), this error seems probable, although no systematic dependency on friction velocity (*u**) has been found. For instance, varying source areas of the CO_2 fluxes ('footprint') might have contributed to the variation in estimated ecosystem respiration.

(ii) The data were pooled into 5-day intervals in order to obtain a relatively large number of data points, which reduces the random error inherent to the eddy covariance measurements by the factor $\sqrt{\text{sample}}$ size (Moncrieff *et al.* 1996; Sachs 1996). While reducing the random error of the measurements, naturally occurring variability is also 'smoothed' out. As respiration depends non-linearly on soil moisture and temperature, aggregation errors must be expected (Lischke *et al.* 1997; Rastetter *et al.* 1992). This error was estimated by applying the fitted respiration model function to the hourly values of temperature and moisture from the soil model and averaging the function over the same period that was used for averaging the driving variables. For both sites, the aggregation error for respiration was less than a 2% overestimate (Reichstein 2001).

(iii) A third source of error is that the predictor variables themselves are a model output, although

the agreement between modelled and measured soil conditions was good.

(iv) Most importantly, the large ecosystem respiration in May/June for Castelporziano, and the underestimation of respiration by the best abiotic model IV in October on the Puéchabon site, indicate that seasonality of biotic processes influences the annual course of ecosystem respiration.

Several biotic factors might contribute to seasonal variability in respiration: phenologically controlled respiration of leaves, roots and rhizosphere (Lavigne *et al.* 1997; Ryan *et al.* 1997); death and regrowth of microbes within drying–rewetting cycles (Orchard & Cook 1983; Pulleman & Tietema 1999); macrofaunal activity (Coleman 1996); and variability in litter fall and root death and, thus, changes in available C pools for decomposition. While (in contrast to deciduous forests) intra-annual changes in LAI are minor at our two evergreen forest sites, growth respiration of fine roots and new leaves may still have contributed to the large ecosystem respiration in May at Castelporziano.

The importance of seasonal variability of soil C pool size appeared to be minor in this study. By applying a dynamic soil organic matter decomposition submodel, the labile pool size varied by 7% maximally, despite sixfold month-to-month changes in litter input. The relatively small inputs cannot significantly influence the overall litter pool for decomposition throughout the season (monthly input is maximally 23% of the litter pool). With changes in pool sizes of 7%, changes in normalized soil microbial respiration were only 5% or $0 \cdot 1 \, \mu\text{mol m}^{-2} \, \text{s}^{-1}$, which is small compared to the residuals of the regression model.

Two C pools may be too few to describe intra-annual dynamics, and rapid decomposition of labile substances could contribute significantly to seasonal variability (e.g. sugars and amino-acids; Kuzyakov & Demin 1998). However, a simple calculation suggests that this is improbable. If we conservatively assume that all the soluble sugar in litter input is decomposed within 1 day, the maximal flux from this compartment would be $6 \, \text{g litter m}^{-2} \, \text{day}^{-1} \times 0 \cdot 5 \times 10^{-3} \, \text{g sugar (g litter)}^{-1} = 3 \cdot 0 \times 10^{-3} \, \text{g sugar m}^{-2} \, \text{day}^{-1} = 1 \cdot 2 \times 10^{-3} \, \text{g sugar C m}^{-2} \, \text{day}^{-1} = 1 \cdot 14 \times 10^{-3} \, \mu\text{mol C m}^{-2} \, \text{s}^{-1}$, which is negligible. In this calculation, a sugar content in the litter of $500 \, \text{mg kg}^{-1}$ was assumed for *Q. ilex* aboveground litter (Gillon *et al.* 1994). Indirect effects of fresh litter ('priming' effect: Anderson & Domsch 1986; Högberg & Ekblad 1996) have not been considered.

It is possible that soil microbial growth dynamics add to the seasonal variability of ecosystem respiration. Merzouki (1986) found an increase in soil microbial biomass C from $2 \cdot 0$ to $3 \cdot 2\%$ of organic C within 2 months (September–November), which corresponds to a flux of $1 \cdot 2\% \times 3 \cdot 25 \, \text{kg C m}^{-2}/2 \, \text{months} = 0 \cdot 63 \, \mu\text{mol C m}^{-2} \, \text{s}^{-1}$. If we further assume microbial C-use efficiency of $0 \cdot 28$, then this results in a respiratory flux due to microbial growth of $0 \cdot 63 \times (1/0 \cdot 28 - 1) = 1 \cdot 62$

μmol m^{-2} s^{-1} (cf. Ågren & Bosatta 1996). This exceeds even the residual of the regression model in these months (Fig. 3). We conclude that microbial growth respiration might contribute more significantly to the seasonality of ecosystem respiration in an evergreen forest than do changing litter pools, and the actual effect should be more thoroughly studied in combination with root growth (Merzouki 1986; Ryan *et al*. 1997). The dynamics of litter pools have more influence on the interannual variability of C fluxes, because the time during which litter pools potentially build up or disappear is longer.

A second reason for applying the soil C balance model (ICBM) was to estimate soil microbial respiration at Puéchabon to make an initial separation from the top-down estimate of ecosystem respiration. The results indicate that microbial respiration was the largest contribution to ecosystem respiration (50%). If we assume that above- and below-ground autotrophic respiration is roughly equal, then root respiration would be 25% of total ecosystem respiration, or one-third of soil plus litter respiration. This agrees with experimental studies in forest and heath ecosystems (Bowden *et al*. 1993; Chapman 1979), but is clearly at the lower end of the 30–70% reported by Raich & Schlesinger (1992) in a global survey. The estimate of soil microbial respiration contributing approximately 50% to ecosystem respiration depends on the reliability of the eddy covariance data and the independent parameterization of the ICBM. If ecosystem respiration was underestimated by the eddy covariance technique by 27%, as in Lavigne *et al*. (1997), soil microbial respiration would still be 40% of total ecosystem respiration, and root respiration would be 42% of total soil respiration, with the same assumption about autotrophic respiration partitioning as above. Another interesting hypothesis from the data-model comparison is that not only decomposition, but also autotrophic respiration, is strongly affected by the drought. For the Puéchabon site, only 0·5 μmol m^{-2} s^{-1} respiration (= observed ecosystem respiration minus modelled decomposition respiration at the end of the drought) would be left for plant respiration at 25–30 °C air temperature. This would mean a considerable reduction in leaf respiration through drought, which is not yet included in models (cf. Baldocchi 1997; Tenhunen *et al*. 1994; Williams *et al*. 1996). This hypothesis is supported by some data (Pereira *et al*. 1986; Tretiach *et al*. 1997). Tretiach *et al*. (1997) studied *Q. ilex* leaves and found small differences in leaf respiration rate between August and October, although air temperature differed by more than 10 °C.

Conclusions

(i) A drought- and temperature-dependent intra-annual time-course of ecosystem respiration was derived from eddy covariance data for two Mediterranean evergreen oak forest sites.

(ii) The Lloyd & Taylor (1994) model for temperature dependence of soil respiration performed well.

(iii) However, a new functional dependence of ecosystem respiration on soil moisture is suggested, with a higher sensitivity at low water contents than in current models.

(iv) In addition, the data reveal that the temperature sensitivity (Q_{10}) of ecosystem respiration increases with soil moisture, so that the validity of commonly used multiplicative models is questioned.

(v) As a conclusion from the application of a C balance model, the intra-annual dynamic of litter pools is likely to have little influence on the seasonality of ecosystem respiration, but microbial growth dynamics might have a larger influence. If these patterns are confirmed at other sites, the modified relationships (points iii and iv) should be included in future C-cycle and climate-change models.

References

Ågren, G.I. & Bosatta, E. (1996) *Theoretical Ecosystem Ecology – Understanding Nutrient Cycles*. Cambridge University Press, Cambridge, UK.

Anderson, J.M. (1991) The effects of climate change on decomposition processes in grassland and coniferous forests. *Ecological Applications* **1**, 326–347.

Anderson, T.-H. & Domsch, K.H. (1986) Carbon link between microbial biomass and soil organic matter. *Perspectives in Microbial Ecology* (eds F. Megusár & M. Gantar), pp. 467–471. Slovene Society for Microbiology, Ljubljana.

Andrén, O. & Kätterer, T. (1997) ICBM – the introductory carbon balance model for exploration of soil carbon balances. *Ecological Applications* **7**, 1226–1236.

Aubinet, M., Grelle, A., Ibrom, A. *et al*. (2000) Estimates of the annual net carbon and water exchange of forests: The EUROFLUX methodology. *Advances in Ecological Research* **30**, 113–175.

Baldocchi, D.D. (1997) Measuring and modelling carbon dioxide and water vapour exchange over a temperate broad-leaved forest during the 1995 summer drought. *Plant, Cell and Environment* **20**, 1108–1122.

Baldocchi, D.D., Valentini, R., Running, S., Oechel, W. & Dahlman, R. (1996) Strategies for measuring and modelling carbon dioxide and water vapour fluxes over terrestrial ecosystems. *Global Change Biology* **2**, 159–168.

Boone, R.D., Nadelhoffer, K., Canary, J.D. & Kaye, J.P. (1998) Roots exert a strong influence on the temperature sensitivity of soil respiration. *Nature* **396**, 570–572.

Borken, W., Xu, Y.J., Brumme, R. & Lamersdorf, N. (1999) A climate change scenario for carbon dioxide and dissolved organic carbon fluxes from a temperate forest soil: drought and rewetting effects. *Soil Science Society of America Journal* **63**, 1848–1855.

Bottner, P., Coûteaux, M.M. & Vallejo, V.R. (1995) Soil organic matter in mediterranean-type ecosystems and global climatic changes: a case study – the soil of the Mediterranean Basin. *Global Change and Mediterranean-Type Ecosystems* (eds J. M. Moreno & W. C. Oechel), pp. 306–325. Springer, Berlin.

Bowden, R.D., Nadelhoffer, K.J., Boone, R.D., Melillo, J.M. & Garrison, J.B. (1993) Contributions of aboveground litter, belowground litter, and root respiration to total soil respiration in a temperate mixed hardwood forest. *Canadian Journal of Forest Research* **23**, 1402–1407.

Bunnell, F.L., Tait, D.E.N., Flanagan, P.W. & van Cleve, K. (1977) Microbial respiration and substrate weight loss – I.

A general model of the influences of abiotic variables. *Soil Biology and Biochemistry* **9**, 33–40.

Carlyle, J.C. & BaThan, U. (1988) Abiotic controls of soil respiration beneath an 18-year-old *Pinus radiata* stand in South-East Australia. *Journal of Ecology* **76**, 654–662.

Casals, P., Romanya, J., Cortina, J., Bottner, P., Couteaux, M.M. & Vallejo, V.R. (2000) CO_2 efflux from a Mediterranean semi-arid forest soil. I. Seasonality and effects of stoniness. *Biogeochemistry* **48**, 261–281.

di Castri, F. (1981) Mediterrnean-type shrublands of the world. *Mediterranean-type Shrublands* (F. Di Castri, D. W. Goodall & R. L. Specht), pp. 1–52. Elsevier, Amsterdam.

Chapman, S.B. (1979) Some interrelationships between soil and root respiration in lowland *Calluna* heathland in southern England. *Journal of Ecology* **67**, 1–20.

Coleman, D.C. (1996) *Fundamentals of Soil Ecology*. Academic Press, San Diego.

Cox, P.M., Betts, R.A., Jones, C.D., Spall, S.A. & Totterdell, I.J. (2000) Acceleration of global warming due to carbon-cycle feedbacks in a coupled climate model. *Nature* **408**, 184–187.

Davidson, E.A., Belk, E. & Boone, R.D. (1998) Soil water content and temperature as independent or confounded factors controlling soil respiration in temperate mixed hardwood forest. *Global Change Biology* **4**, 217–227.

Deutschmann, G., Malessa, V. & Rummenhohl, H. (1994) Bestimmung der Lagerungsdichte in stark skeletthaltigen Böden. *Zeitschrift für Pflanzenernährung und Bodenkunde* **157**, 77–79.

Draper, N. & Smith, H. (1981) *Applied Regression Analysis*. Wiley, New York.

Efron, B. & Tibshirani, R.J. (1993) *An Introduction to the Bootstrap*. Chapman & Hall, New York, NY.

Epron, D., Farque, L., Lucot, E. & Badot, P.-M. (1999) Soil CO_2 efflux in a beech forest: dependence on soil temperature and soil water content. *Annals of Forest Science* **56**, 221–226.

Fang, C. & Moncrieff, J.B. (1999) A model for soil CO_2 production and transport 1: model development. *Agricultural and Forest Meteorology* **95**, 225–236.

van Genuchten, M.T. (1980) A closed-form equation for predicting the hydraulic conductivity of unsaturated soils. *Soil Science Society of America Journal* **44**, 892–898.

Gillon, D., Joffre, R. & Ibrahima, A. (1994) Initial litter properties and decay rate: a microcosm experiment on Mediterranean species. *Canadian Journal of Botany* **72**, 946–954.

Hanson, P.J., Wullschleger, S.D., Bohlmann, S.A. & Todd, D.E. (1993) Seasonal and topographic patterns of forest floor CO_2 efflux from an upland oak forest. *Tree Physiology* **13**, 1–15.

Högberg, P. & Ekblad, A. (1996) Substrate-induced respiration measured *in situ* in a C_3-plant ecosystem using additions of C_4-sucrose. *Soil Biology and Biochemistry* **28**, 1131–1138.

Janssen, P.H.M. & Heuberger, P.S.C. (1995) Calibration of process oriented models. *Ecological Modelling* **83**, 55–66.

Joffre, R., Rambal, S. & Romane, F. (1996) Local variations of ecosystem functions in Mediterranean evergreen oak woodland. *Annales des Sciences Forestales* **53**, 561–570.

Johnson, L.C., Shaver, G.R., Giblin, A.E. *et al.* (1996) Effects of drainage and temperature on carbon balance of tussock tundra microcosms. *Oecologia* **108**, 737–748.

Jones, M.H., Fahnestock, J.T., Stahl, P.D. & Welker, J.M. (2000) A note on summer CO_2 flux, soil organic matter, and microbial biomass from different High Arctic ecosystem types in Northwestern Greenland. *Arctic, Antarctic and Alpine Research* **32**, 104–106.

Kätterer, T., Reichstein, M., Andrén, O. & Lomander, A. (1998) Temperature dependence of organic matter decomposition: a critical review using literature data analysed with different models. *Biology and Fertility of Soils* **27**, 258–262.

Keith, H., Jacobsen, K.L. & Raison, R.J. (1997) Effects of soil phosphorus availability, temperature and moisture on soil respiration in *Eucalyptus pauciflora* forest. *Plant and Soil* **190**, 127–141.

Kirschbaum, M.U.F. (1995) The temperature dependence of soil organic matter decomposition, and the effect of global warming on soil organic carbon storage. *Soil Biology and Biochemistry* **27**, 753–760.

Kuzyakov, Y. & Demin, V. (1998) CO_2 efflux by rapid decomposition of low molecular organic substances in soils. *Sciences of Soils* **3**, 1–7.

Lavigne, M.B., Ryan, M.G., Anderson, D.E. *et al.* (1997) Comparing nocturnal eddy covariance measurements to estimates of ecosystem respiration made by scaling chamber measurements. *Journal of Geophysical Research* **102**, 28977–28986.

Leirós, M.C., Trasar-Cepada, C., Seoane, S. & Gil-Sotres, F. (1999) Dependence of mineralization of soil organic matter on temperature and moisture. *Soil Biology and Biochemistry* **31**, 327–335.

Lischke, H., Loeffler, H.J. & Fischlin, A. (1997) Calculating temperature dependence over long time periods: a comparison and study of methods. *Agricultural and Forest Meteorology* **86**, 169–181.

Liski, J., Ilvesniemi, H., Mäkelä, A. & Westman, K.J. (1999) CO_2 emissions from soil in response to climatic warming are overestimated – the decomposition of old soil organic matter is tolerant of temperature. *Ambio* **28**, 171–174.

Lloyd, J. & Taylor, J.A. (1994) On the temperature dependence of soil respiration. *Functional Ecology* **8**, 315–323.

Lossaint, P. & Rapp, M. (1978) La forêt Méditerranéene de Chênes verts. *Structure et Fonctionnement Des Écosystemémes Terrestres* (eds M. Lamotte & F. Bourliére), pp. 129–183. Masson, Paris.

Manes, F., Grignetti, A., Tinelli, A., Lenz, R. & Ciccioli, P. (1997) General features of the Castelporziano test site. *Atmospheric Environment* **31**, 19–25.

Marshall, T.J. & Holmes, J.W. (1988) *Soil Physics*. Cambridge University Press, Cambridge.

Merzouki, A. (1986) Les effets d'une coupe a blanc sur l'activité biologique d'un sol fersiallitique méditerraneén. PhD Dissertation, CEFE-CNRS, Montpellier.

Moldrup, P., Rolston, D.E. & Hansen, A.A. (1989) Rapid and numerically stable simulation of one dimensional, transient water flow in unsaturated, layered soils. *Soil Science* **148**, 219–226.

Moldrup, P., Rolston, D.E., Hansen, A.A. & Yamaguchi, T. (1991) A simple, mechanistic model for soil resistance to plant water uptake. *Soil Science* **151**, 87–93.

Moncrieff, J.B., Malhi, Y. & Leuning, R. (1996) The propagation of errors in long-term measurements of land-atmosphere fluxes of carbon and water. *Global Change Biology* **2**, 231–240.

Norman, J.M., Garcia, R. & Verma, S.B. (1992) Soil surface CO_2 fluxes and the carbon budget of a grassland. *Journal of Geophysical Research* **97**, 18845–18853.

Orchard, V.A. & Cook, F.J. (1983) Relationship between soil respiration and soil moisture. *Soil Biology and Biochemistry* **15**, 447–454.

Pereira, J.S., Tenhunen, J.D., Lange, O.L., Beyschlag, W., Meyer, A. & David, M.M. (1986) Seasonal and diurnal patterns in leaf gas exchange of *Eucalyptus globulus* trees growing in Portugal. *Canadian Journal of Forest Research* **16**, 177–184.

Pinol, J., Alcaniz, J.M. & Roda, F. (1995) Carbon dioxide efflux and pCO_2 in soils of three *Quercus ilex* montane forests. *Biogeochemistry* **30**, 191–215.

Pulleman, M. & Tietema, A. (1999) Microbial C and N transformations during drying and rewetting of coniferous forest floor material. *Soil Biology and Biochemistry* **31**, 275–285.

Raich, J.W. & Schlesinger, W.H. (1992) The global carbon dioxide flux in soil respiration and its relationship to vegetation and climate. *Tellus* **44B**, 81–99.

Rastetter, E.B., King, A.W., Cosby, B.J., Hornberger, G.M., O'Neill, R.V. & Hobbie, J.E. (1992) Aggregating fine scale ecological knowledge to model coarser-scale attributes of ecosystems. *Ecological Applications* **2**, 55–70.

Reichstein, M. (2001) Drought effects on ecosystem gas exchange in three Mediterranean ecosystems. A combined top-down and bottom-up analysis of eddy covariance data. PhD Dissertation, University of Bayreuth.

Reichstein, M., Bednorz, F., Broll, G. & Kätterer, T. (2000) Temperature dependence of carbon mineralization: conclusions from a long-term incubation of subalpine soil samples. *Soil Biology and Biochemistry* **32**, 947–958.

Rovira, P. & Vallejo, V.R. (1997) Organic carbon and nitrogen mineralization under Mediterranean climatic conditions: the effects of incubation depth. *Soil Biology and Biochemistry* **29**, 1509–1520.

Ryan, M.G., Lavigne, M.B. & Gower, S.T. (1997) Annual carbon cost of autotrophic respiration in boreal forest ecosystems in relation to species and climate. *Journal of Geophysical Research* **102D**, 28871–28883.

Sachs, L. (1996) Angewandte Statistik. *Anwendung Statistischer Methoden*. Springer, Berlin.

Schlentner, R.E. & van Cleve, K. (1985) Relationship between CO_2 evolution from soil, substrate temperature, and substrate moisture in four mature forest types in interior Alaska. *Canadian Journal of Forest Research* **15**, 97–106.

Tenhunen, J.D., Harley, P.C., Beyschlag, W. & Lange, O.L. (1987) Changes during summer drought in leaf CO_2 uptake rates of macchia shrubs growing in Portugal: limitations due to photosynthetic capacity, carboxylation efficiency, and stomatal conductance. *Plant Responses to Stress* (eds J. D. Tenhunen, F. M. Catarino, O. L. Lange & W. C. Oechel), pp. 305–327. Springer, Berlin.

Tenhunen, J.D., Siegwolf, R.A. & Oberbauer, S.F. (1994) Effects of phenology, physiology, and gradients in community composition, structure, and microclimate on tundra ecosystems. *Ecophysiology of Photosynthesis*, Ecological Studies 100 (eds E. D. Schulze & M. M. Caldwell), pp. 431–460. Springer, Berlin.

Tretiach, M., Bolognini, G. & Rondi, A. (1997) Photosynthetic activity of *Quercus ilex* at the extremes of a transect between Mediterranean and submediterranean vegetation (Trieste–NE Italy). *Flora* **192**, 369–378.

Valentini, R., Scarascia Mugnozza, G. & Ehleringer, J.R. (1992) Hydrogen and carbon isotope ratios of selected species of a mediterrenean macchia ecosystem. *Functional Ecology* **6**, 627–631.

Valentini, R., Matteucci, G., Dolman, A.J. *et al.* (2000) Respiration as the main determinant of carbon balance in European forests. *Nature* **404**, 861–865.

Visual Numerics, Inc. (1993) *PV-WAVE Advantage*. Visual Numerics, Houston, TX.

Vourlitis, G.L. & Oechel, W.C. (1999) Eddy covariance measurements of CO_2 and energy fluxes of an Alaskan tussock tundra ecosystem. *Ecology* **80**, 686–701.

Williams, M., Rastetter, E.B., Fernandes, D.N. *et al.* (1996) Modelling the soil–plant–atmosphere continuum in a *Quercus–Acer* stand at Harvard Forest: the regulation of stomatal conductance by light, nitrogen and soil/plant hydraulic properties. *Plant, Cell and Environment* **19**, 911–927.