

Seasonal and annual variation of carbon exchange in an evergreen Mediterranean forest in southern France

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Abstract

We present 9 years of eddy covariance measurements made over an evergreen Mediterranean forest in southern France. The goal of this study was to quantify the different components of the carbon (C) cycle, gross primary production (GPP) and ecosystem respiration (R_{eco}), and to assess the effects of climatic variables on these fluxes and on the net ecosystem exchange of carbon dioxide. The Puéchabon forest acted as a net C sink of $-254 \text{ g C m}^{-2} \text{ yr}^{-1}$, with a GPP of $1275 \text{ g C m}^{-2} \text{ yr}^{-1}$ and a R_{eco} of $1021 \text{ g C m}^{-2} \text{ yr}^{-1}$. On average, 83% of the net annual C sink occurred between March and June. The effects of exceptional events such the insect-induced partial canopy defoliation that occurred in spring 2005, and the spring droughts of 2005 and 2006 are discussed. A high interannual variability of ecosystem C fluxes during summer and autumn was observed but the resulting effect on the annual net C budget was moderate. Increased severity and/or duration of summer drought under climate change do not appear to have the potential to negatively impact the average C budget of this ecosystem. On the contrary, factors affecting ecosystem functioning (drought and/or defoliation) during March–June period may reduce dramatically the annual C balance of evergreen Mediterranean forests.

Keywords: CO₂ fluxes, eddy covariance, Mediterranean ecosystem, *Quercus ilex*

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Introduction

At a global scale, Mediterranean-type ecosystems (MTE) cover $2.5 \times 10^6 \text{ km}^2$ (Hobbs *et al.*, 1995) mainly dominated by evergreen sclerophyllous forests. This biome is highly represented in southern Europe, particularly in southern France (21 860 km²), Spain (92 000 km²) and Italy (15 700 km²). In these areas, *Quercus ilex* forests are one of the major dominant species (Terradas, 1999). The Mediterranean climate is characterized by mild winter temperatures concomitant with the rainy period as opposed to severe summer droughts and heat (Barbero *et al.*, 1992) but also displays high interannual variation of rainfall and temperature. This climate induces a long growing season interrupted during summer when water stress reaches an extent that dramatically limits ecosystem functioning (Reichstein *et al.*, 2002). Another characteristic of Mediterranean

ecosystems relies on the ‘evergreenness’ of most dominant species. This feature allows the ecosystem to stay active during the wet period when temperature and solar radiation are suboptimal (Warren & Adams, 2004).

The Mediterranean basin has long been recognized as a model region for studying global change effects on terrestrial ecosystems (Lavorel *et al.*, 1998). Recent climate projections forecast a >20% decline in precipitation in the Mediterranean basin (Giorgi, 2006; Rowell & Jones, 2006) mainly during the summer period accompanied by more frequent and more intense heatwaves. Mediterranean ecosystems are likely to experience more frequent and intense, as well as longer drought (Christensen *et al.*, 2007). How these changes could affect ecosystem functioning and how that could trigger a positive feedback on climate by modifying carbon dioxide (CO₂) sequestration in ecosystems is a keystone question for comprehending atmospheric changes in the on-going century.

Net ecosystem exchange (NEE) of CO₂ between the biosphere and the atmosphere results from the differ-

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ence between two large fluxes: gross primary production (GPP) and ecosystem respiration (R_{eco}). Because GPP and R_{eco} display partially distinct responses to climate drivers (Reichstein *et al.*, 2002), predicting the response of NEE to fluctuating environmental conditions is complex. The evaluation of climate change effects on NEE requires a detailed understanding of the underlying processes which govern ecosystem function. Therefore, measurements of ecosystem CO₂ fluxes are required under a sufficient range of environmental conditions in order to derive robust generalizations about the C budget of Mediterranean forests.

The C budget of different MTE have already been studied, including grasslands (Xu & Baldocchi, 2004; Ma *et al.*, 2007; Pereira *et al.*, 2007), shrubland (Serrano-Ortiz *et al.*, 2007), oak savanna, (Ma *et al.*, 2007) and evergreen forests (Miglietta & Peressotti, 1999; Grunzweig *et al.*, 2003; Tirone *et al.*, 2003). Nevertheless, we believe information is still lacking in particular regarding the effects of exceptional climatic events on carbon (C) fluxes in these ecosystems that require sufficiently long dataset to capture both average and exceptional climatic years.

Our study is based on a 9-year dataset of NEE measurements carried out at the Puéchabon *Q. ilex* forest in the south of France. This large dataset provides the opportunity to study the effects of climate on interannual variation of actual evapotranspiration (ET), NEE, and its constitutive fluxes (GPP and R_{eco}).

Materials and methods

Site description

The study site was located 35 km NW of Montpellier (southern France) in the Puéchabon State Forest (3°35'45''E, 43°44'29''N, elevation = 270 m) on a flat plateau. This forest has been managed as a coppice for centuries and was last cut in 1942. Vegetation was largely dominated by a dense overstorey of the evergreen tree *Q. ilex*. Mean tree height was about 5 m. In 2005, the density of resprouted stem was 6885 stems ha⁻¹. Stems with a diameter at breast height (DBH) <4 cm represented 12% of the total stems, whereas stems with DBH >10 cm represented 12.5% of the total stems. Aboveground biomass was 12.3 kg dry matter (DM) m⁻² in 2005. Understorey species compose a sparse (<25%) shrubby <2 m high layer with *Buxus sempervirens*, *Phyllirea latifolia*, *Pistacia terebinthus*, and *Juniperus oxycedrus* being the most abundant species. Overstorey leaf area index (LAI = 2.8 ± 0.4) was evaluated using a LAI 2000 leaf area meter (Li-Cor Inc., Lincoln, NE, USA) twice a year since 1999 in the neighborhood of the flux tower.

The Puéchabon forest has a Mediterranean-type climate, with a mean annual rainfall of 907 mm yr⁻¹, with a range of 546–1549 mm for the 1984–2006 period. Precipitation mainly occurs during autumn and winter with about 80% of the annual rainfall occurring between September and April (Fig. 1). Mean annual temperature over the same period was 13.4 °C with a minimum in January (5.5 °C) and a maximum in July (22.9 °C).

The soil is extremely rocky from hard Jurassic limestone parent material; on average the volumetric fractional content of stones and rocks is about 0.75 for the top 0–50 cm and 0.90 below. The stone free fraction of the soil is a homogeneous silty clay loam (USDA texture triangle) in the 0–50 cm layer (38.8% clay, 35.2% silt, and 26% sand). The soil fills up the space between the stones and rocks and this provides a source of water throughout the long dry summers for the deep-rooted *Q. ilex*. About 90% of the root mass can be found in the first 50 cm but some roots have been found up to 4.5 m deep.

Flux measurements

The site was part of the CARBOEUROPE-IP (<http://www.carboeurope.org>) European project within the framework of the global network FLUXNET (<http://daac.ornl.gov/FLUXNET/>). Eddy covariance fluxes of CO₂, sensible heat (H), latent heat (LE), and momentum (τ) were measured at a half hourly time step from July 1998 to December 2006 (with an 8-month interruption between November 1999 and July 2000) at a height of 11 m (about 6 m above the top of the dominant tree species). The eddy covariance facility included a three-dimensional sonic anemometer (Solent R2 during the 1998–1999 periods and R3 since 2000, Gill Instruments, Lymington, UK) and a closed path infrared gas analyzer (IRGA, model LI 6262, Li-Cor Inc.), both sampling at a rate of 21 Hz. Flux data were processed following Aubinet *et al.* (2000). Approximately 11% of the potential data was lost each year due to maintenance or instrument failure.

Data processing

High-frequency losses due to our closed-path system were quantified by spectral analysis and the corresponding corrections (6% for H₂O and 1% for CO₂) were applied. Data were filtered following CARBOEUROPE-IP quality check recommendations including the stationary test and the integral turbulence test. Approximately 14% of the data were discarded as a result. Night-time data were also filtered for low friction velocity (u^*), discarding values with $u^* < 0.35 \text{ m s}^{-1}$

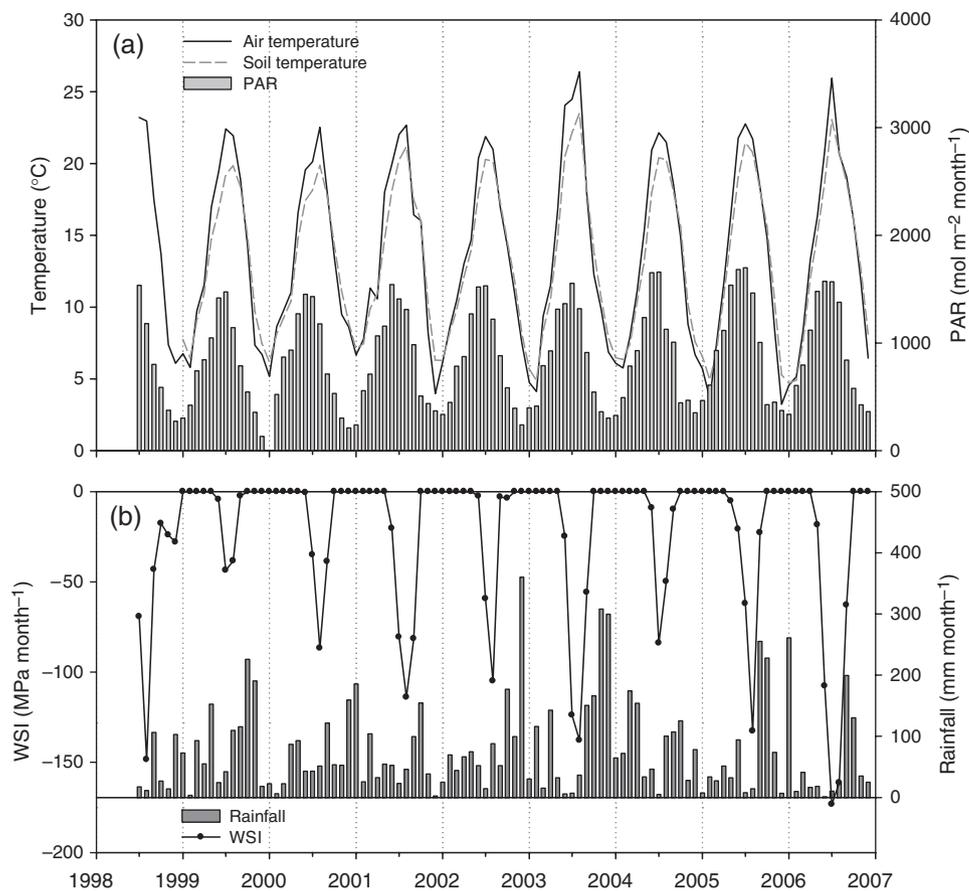


Fig. 1 Temporal course of (a) air and soil temperature and PAR and (b) water stress integral (WSI) and rainfall at the Puéchabon site between July 1998 and December 2006. PAR, photosynthetically active radiation.

(threshold determined empirically, data not shown) to minimize measurement bias associated with insufficient turbulent mixing. Between 30% and 40% of half hourly data of CO_2 , τ , LE, and H fluxes were eliminated after filtering. In order to fill missing data resulting from technical problems and quality check filtering the gap-filling algorithm developed by Reichstein *et al.* (2005) was used. The program is accessible online at: <http://gaia.agraria.unitus.it/database/eddyproc/>

This method is based on modified procedures from Falge *et al.* (2001). The partitioning of NEE into GPP and R_{eco} was also performed using this tool based on the flux-partitioning algorithm described in Reichstein *et al.* (2005). The procedure was based on the short-term temperature sensitivity of R_{eco} , and thus, largely avoids the bias introduced by confounding factors (growth dynamic, drought effect) in seasonal data. In order to characterize the flux contribution from the land cover type and verify that the basic theoretical assumptions of flux measurements are valid, 2001 flux data were checked using a combination of an analytical footprint model and quality test applied on the flux momentum,

sensible and LE and on the CO_2 flux (Rebmann *et al.*, 2005).

Environmental variables

Half-hourly data of air temperature, relative humidity, solar global radiation, photosynthetically active photon flux density, net radiation balance, rainfall, soil heat flux, and heat storage in the tree trunks (only for the 1998–1999 period) were recorded using a data logger (model 21X, Campbell Scientific Ltd, Shepshed, UK) and installed near the eddy covariance system on the top of the flux tower. Samples were taken every 1 min and aggregated on half-hourly basis. Soil water status in the 0–4.5 m profile was evaluated monthly using a neutron moisture gauge (model DMG 11 Ronly Electronics Ltd, Rishon Lezion, Israel and from July 2001 with a CPN503, Campbell Pacific Nuclear Int., Martinez, CA, USA). The soil water storage was computed by numerical integration of the profile of soil water content and then averaged from six profiles distributed across the site. Soil water storage were interpolated using a soil

water balance model (see detailed description in Rambal, 1993). Superficial (0–15 cm) soil relative water content was measured weekly with a TDR (TRASE system, model 6050X1, Soil moisture, Goleta, CA, USA) at 18 points within 20 m of the flux tower. Comparison of measured against simulated soil water storage showed very good agreement (Rambal *et al.*, 2003). Water stress integral (WSI) is a cumulative index of drought severity and duration. It was calculated following Myers (1988) using measured and modeled soil water potential data.

A standard weather station was located in a tree-free area, 230 m east of the eddy covariance equipment and provided long-term climatic data (1984–2006). Environmental data from this station were closely related to those from the 12 m height station but for air temperature data that exhibited slightly more amplitude at the ground level.

Statistical analysis

Nonlinear and linear regressions for GPP and R_{eco} model fitting were performed with the SIGMAPLOT 2002 (v8.0) statistical package.

Results

Climate

The climate of Puéchabon during the monitoring period was typical of the Mediterranean area, characterized by hot and dry summers, rainy springs, and autumns and mild and relatively dry winters (Fig. 1). The rainfall pattern at this site was associated with a strongly seasonal course of WSI as predicted by the model described in 'Materials and methods' (Fig. 1b). The greatest water stress usually occurred in August with a WSI of $-103 \text{ MPa month}^{-1}$ on average over the 9 years of the experiment (Fig. 2d). Mean annual rainfall over the 1998–2006 experimental periods was 903 mm yr^{-1} , nearly identical than that of the long-term 1984–2006 dataset (905 mm). Autumnal rainfall was characterized by occasional violent storms that provided up to $80 \text{ mm rainfall day}^{-1}$ (data not shown). The interannual variability was strong with a particularly dry year in 1998 (578 mm) while in 2003 the rainfall reached 1310 mm (Fig. 1b). Short-term anomalies were also recorded. The summers of 1999 and 2004 were characterized by more rainfall than the experimental period mean with 110 and 100 mm in August 1999 and 2004, respectively (Fig. 1b). This resulted in lower than normal levels of moisture stress with WSI values during these periods of -38 , and $-50 \text{ MPa month}^{-1}$ in August 1999, 2004, respectively (Fig. 1b). The rainfall pattern

was very unusual in 2005, only 268 mm of rainfall was recorded during the first 8 months of the year, compared with 439 mm during the same period on average over 1998–2006. In 2006, an even more important rainfall deficit occurred between February and July with only 97 mm of rainfall, less than the third of the 323 mm recorded for an average year (Fig. 1b). The mean annual air temperature during the experimental period was $13.2 \text{ }^{\circ}\text{C}$; this value was close to the 1984–2006 average of $13.4 \text{ }^{\circ}\text{C}$. The 2003 summer was much warmer than the 22 years average with June, July and August being warmer by 3.3, 2.5, and $4.3 \text{ }^{\circ}\text{C}$, respectively (Fig. 1a).

C balance

Net CO₂ exchange exhibited a clear seasonal pattern despite high interannual variation. Monthly means of NEE pooled over the experimental period characterize the NEE pattern of an average year (Fig. 2a). From January to July the ecosystem acted as a CO₂ sink, on average the maximum C sink activity occurred in April and June with about $-58 \text{ g C m}^{-2} \text{ month}^{-1}$. In average, 16% of the annual C sink occurred during January and February and 82% ($209 \text{ g C m}^{-2} \text{ month}^{-1}$) between March and June. The net CO₂ exchange budget in August and October were slightly positive indicating a moderate C source activity but the balance of C of the ecosystem was near zero from August to December (Fig. 2a) but variability during this period was critical for determining the magnitude of annual NEE (Fig. 5a and b). On average, $254 \text{ g C m}^{-2} \text{ yr}^{-1}$ were sequestered in the ecosystem as shown by the annual cumulative budget of NEE (Fig. 2a). The distributions of R_{eco} and GPP along the year were clearly asymmetric (Fig. 2b). GPP displayed a rapid increase during the January to June period (from -62 to -170 g C m^{-2}) while R_{eco} only increased from 52 to 121 g C m^{-2} during the same period (Fig. 2b). After a dramatic decrease of both fluxes during the July–September period, both exhibited a similar pattern during the last part of the year with a slight increase in September and October and a decrease during the last 2 months. Yearly integrals of GPP and R_{eco} reached -1275 and $1021 \text{ g C m}^{-2} \text{ yr}^{-1}$, respectively based on the monthly average obtained from the full experimental period.

Interannual variation of the annual budget of NEE, GPP, and R_{eco} is presented in Table 1 for the 6 years for which an annual budget could be calculated (2001–2006). Net CO₂ exchange varied from -149 to $-451 \text{ g C m}^{-2} \text{ yr}^{-1}$ in 2006 and 2004, respectively (Table 1). Over these 6 years, the coefficient of variation for NEE was large (42%). The coefficient of variation for GPP was lower (17%) with a minimum (in absolute terms) of $-945 \text{ g C m}^{-2} \text{ yr}^{-1}$ in 2006 and a maximum of

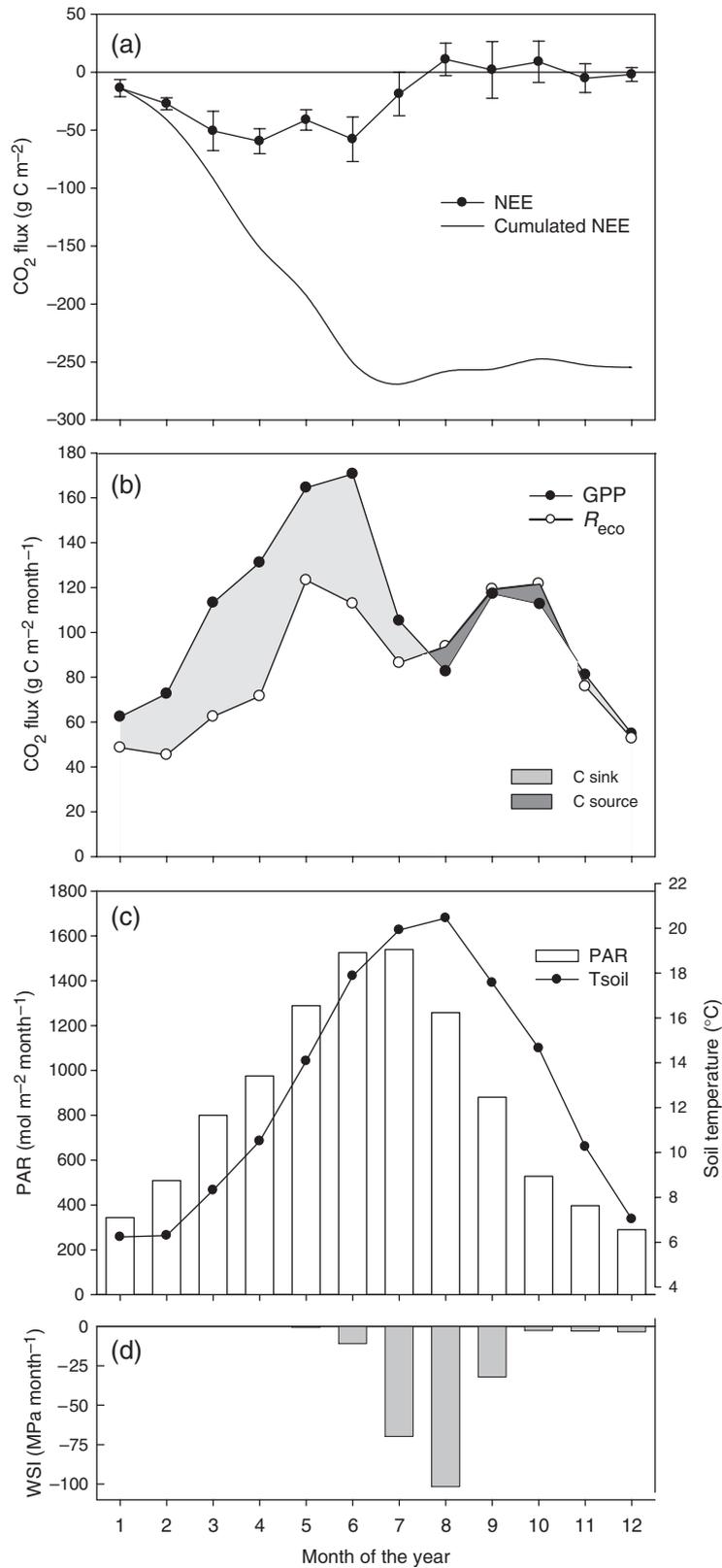


Fig. 2 Monthly average of (a) net ecosystem exchange of CO₂ (NEE) and cumulated NEE at the Puéchabon site, (b) gross primary productivity (GPP; filled circle), ecosystem respiration (R_{eco}; open circle), (c) PAR and soil temperature and (d) water stress integral values are means ± 95% confidence interval of monthly values of 9 consecutive years (1998–2006). PAR, photosynthetically active radiation.

Table 1 Yearly budgets of NEE, GPP, R_{eco} and ET for the six complete years of measurement

Year	NEE (g C m ⁻²)	GPP (g C m ⁻²)	R_{eco} (g C m ⁻²)	ET (mm)
2001	-291.4	1385.8	1094.4	411.8
2002	-352.9	1424.0	1071.1	484.7
2003	-274.5	1302.8	1028.3	360.9
2004	-451.4	1474.5	1023.1	414.4
2005	-149.6	1053.2	903.6	345.7
2006	-149.2	1264.3	986.1	342.3

NEE, net ecosystem exchange; GPP, gross primary production; ET, evapotranspiration; R_{eco} , ecosystem respiration.

-1474 g C m⁻² yr⁻¹ in 2004. R_{eco} was relatively stable compared with GPP over the 6 years (cv = 12%) with all values within the range of 904–1094 g C m⁻² yr⁻¹ (Table 1).

Figure 3a shows the relation between monthly GPP and incident photosynthetically active radiation (PAR) for the 1998–2006 periods. GPP can be described as a nonrectangular hyperbola, which for nonwater stressed months during the 1998–2006 periods can be written

$$\text{GPP} = -0.3 \times \text{PAR} \times \frac{-351.3}{-358.7 - 0.3 \times \text{PAR}} + 0 \quad (r^2 = 0.85, P < 0.0001).$$

In 2005 the relation between GPP and PAR was negatively affected by a *Limantria* (caterpillar) attack (Fig. 3a) that reduced the ecosystem LAI from 5% to 16% according to the sector of the forest (data not shown)

$$\text{GPP} = -0.16 \times \text{PAR} \times \frac{-320.3}{-320.3 - 0.16 \times \text{PAR}} + 0 \quad (r^2 = 0.77, P = 0.005).$$

In case of water stress (WSI < -30 MPa month⁻¹), GPP was independent of incident PAR but linearly related to WSI (Fig. 3b)

$$\text{GPP} = -0.7 \times \text{PAR} - 155.8 \quad (r^2 = 0.64, P < 0.0001).$$

The relation between R_{eco} and soil temperature followed a Q_{10} -type function for the months without water stress (Fig. 3c). 2005 data did not deviate significantly from this relation

$$R_{\text{eco}} = 32.9 \times 2.2^{\frac{T_{\text{soil}} - 10}{10}} \quad (r^2 = 0.73, P < 0.0001).$$

R_{eco} measured during water-limited months, exhibited a linear relation with top-soil water content (Fig. 3d).

$$R_{\text{eco}} = 159 \times \text{RWC} - 12.5 \quad (r^2 = 0.65, P < 0.0001).$$

Water budget

Ecosystem ET present the same pattern as GPP with a peak in June and reaches its minimum in December or January (data not shown). Based on the 1998–2006 period, the mean yearly ET reached 393 mm yr⁻¹, with a minimum of 342 mm in 2006 and a maximum 485 mm in 2002 (Table 1). The coefficient of variation for yearly ET was 14%.

Energy budget

The energy budget of the ecosystem calculated on the half-hourly data of latent and sensible heat, net radiation (measured with a REBS Q7 sensor, Li-Cor Inc., Lincoln, NE, USA) and soil energy storage indicated a lack of closure. On average over the full period the energy budget was closed at 77% and no significant interannual variation was observed (data not shown).

Discussion

Data quality

Following the footprint analysis described in 'Materials and methods', it appeared that more than 80% of the measured fluxes originated from the land use intended to be observed: a dense *Q. ilex* coppice (Rebmann *et al.*, 2005). Moreover, neighboring vegetation is still dominated by *Q. ilex*, but with lower LAI. Clearly, the effect of nonspecific flux to the C budget was marginal. No seasonal pattern of footprint location was detected. In addition, quality tests were made on the fluxes of momentum, sensible and LH and CO₂ and showed that more than 80% of these fluxes could be classified in the 'high quality' data class (Rebmann *et al.*, 2005) thus minimizing error propagation through gapfilling.

The lack of closure of the energy balance observed at this site was similar to that observed in other sites of the EUROFLUX (Aubinet *et al.*, 2000) and FLUXNET (Wilson *et al.*, 2002) networks using similar methods (closed path analyser Licor 6262 and REBS Q7 net radiation sensor). The closure of energy balance was independent of wind direction or incoming radiation and no intraannual pattern of closure was recorded during the 9 years of measurements. As pointed out by Wilson *et al.* (2002), closure of the energy budget is more likely in case of instability or neutral conditions (Z/L < 0.04) compared with stable conditions. In the best conditions (instability and u^* higher than 1 m s⁻¹), the closure of the energy budget reached 86%. Stable conditions generally occur at night and represent about one-third of the measurements periods at this site. The sensibility of the flux sum estimates presented in this study to the

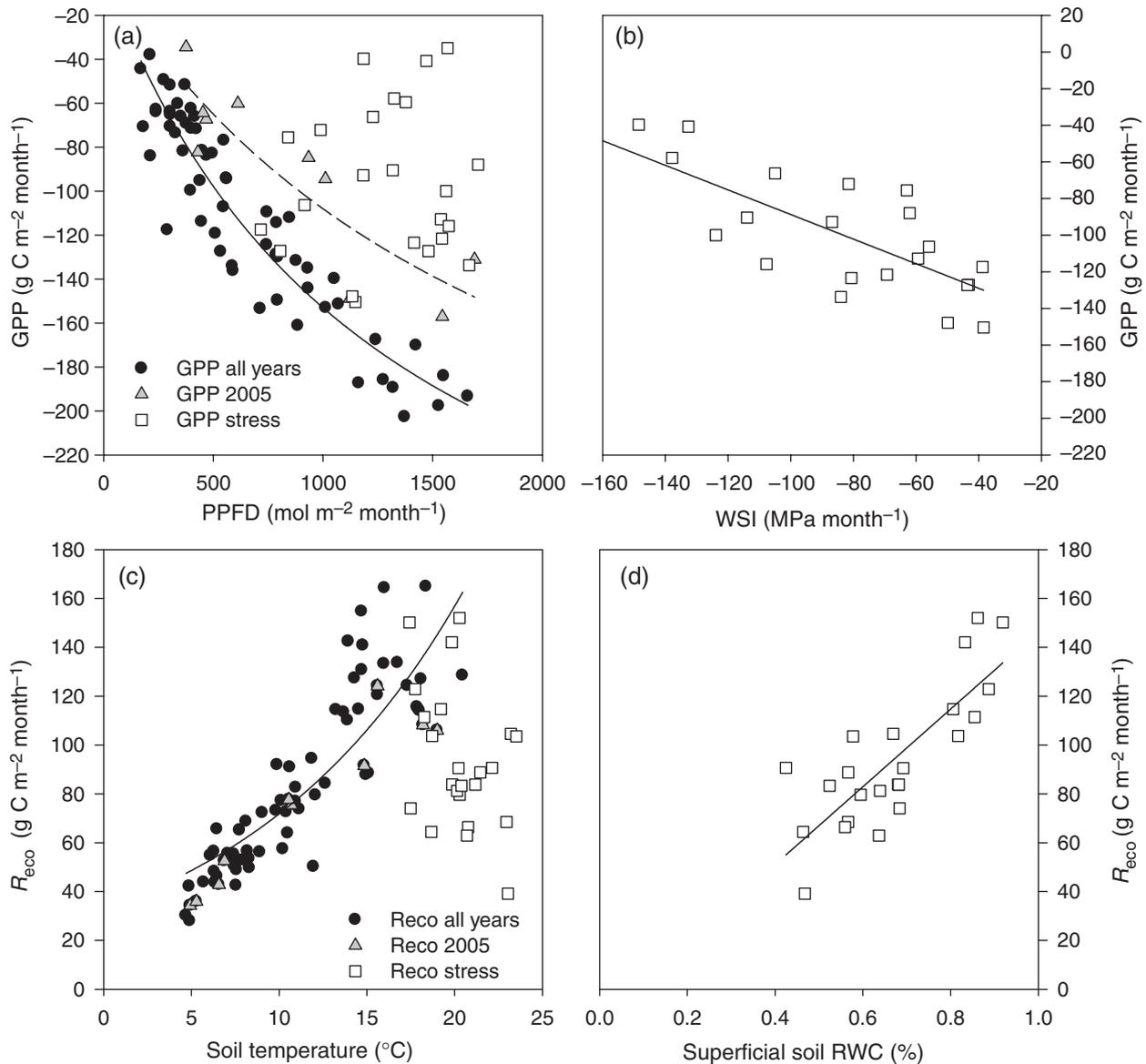


Fig. 3 Relation between monthly integrals of ecosystem C fluxes (a and b, GPP; c and d, R_{eco}) and environmental drivers [a, PAR; b, WSI; c, soil temperature and d, superficial soil relative water content (RWC)]. Black and gray symbols figure available monthly integrals for the 1998–2006 period and 2005 respectively for WSI monthly values of WSI > -30 (no water stress). White symbols figure monthly integral over the full experimental period when WSI < -30 (water stress). PAR, photosynthetically active radiation; WSI, water stress integral; GPP, gross primary productivity.

u^* threshold determination was also tested. The choice of a threshold at $u^* = 0.22$ as proposed in Papale *et al.* (2006) rather than our own, more conservative estimate ($u^* = 0.35$) led to a -13%, -3% and -5% difference on the 2002 annual flux sum for NEP, GPP, and R_{eco} . Clearly, the data-filtering strategy impacts on the magnitude of the flux estimates in all flux studies but, in this particular case, the calculated differences are in the order of magnitude for uncertainty in C balance yet published (Aubinet *et al.*, 2000; Falge *et al.*, 2001).

Annual C budget of Mediterranean ecosystems

Net CO_2 exchange, as measured by the eddy covariance method, provides a measure of the difference between C flows entering the ecosystem (GPP) and C ecosystem output (R_{eco} – which includes both autotrophic and heterotrophic respiration). When fluxes of organic C (e.g. harvesting) at the system boundaries and occasional disturbance (e.g. fire) can be neglected, NEE is an estimate of Net Ecosystem Productivity (NEP), and thus

total ecosystem C budget (Curtis *et al.*, 2002). Most eddy covariance studies, in particular in forests, showed that ecosystems are net sinks for atmospheric CO₂ (Falge *et al.*, 2002a). While systematic uncertainties associated with flux measurements cannot be totally discarded, these observations fit well with other observations demonstrating a large northern hemisphere terrestrial C sink activity (Ciais *et al.*, 1995; Curtis *et al.*, 2002). Our dataset shows that Mediterranean evergreen forests contribute strongly to this global C sink. Over the full experimental period, the *Q. ilex* forest presented in this study acted as a net C sink of $-254 \text{ g C m}^{-2} \text{ yr}^{-1}$ (Fig. 2a). Based only on the six fully recorded years, average annual NEE was $-278 \pm 117 \text{ g C m}^{-2} \text{ yr}^{-1}$ (Table 1).

These results provide a good basis for understanding C sequestration in Mediterranean ecosystems. *Q. ilex* forests are one of the major ecosystems of the east of the Mediterranean basin and cover 2.510^3 km^2 in the south of France, 3.710^3 km^2 in Italy, 1010^3 km^2 in Spain and 1410^3 km^2 in Morocco (Terradas, 1999). The C sink activity observed in Puéchabon, is comparable with the data obtained in other forest sites submitted to a Mediterranean-type climate (Table 2). Two other sites, including a shrubland in Sardinia (Italy) and an sparse *Q. ilex* forest in Portugal with very similar climatic patterns display lower NEP with $-70 \text{ g C m}^{-2} \text{ yr}^{-1}$ (Miglietta & Peressotti, 1999) and $-150 \text{ g C m}^{-2} \text{ yr}^{-1}$ (Pereira *et al.*, 2007), in the Italian and Portuguese sites, respectively (Table 2), but these differences are associated with lower annual rainfall. A *Q. ilex* forest located in Italy (Castelporziano) exhibited a NEP comprised between -547 and $-660 \text{ g C m}^{-2} \text{ yr}^{-1}$ (Valentini *et al.*, 2000; Tirone *et al.*, 2003). Despite a lower annual rainfall at this site, more than two times more C is fixed each year. This apparent discrepancy can be explained by the presence of a shallow ground water table that reduces water limitation during the summer (Tirone *et al.*, 2003). This lower summer water stress can be observed by considering the period of the year at which minimum daily GPP is measured. While the Italian site displayed a maximum GPP limitation during winter due to low PAR levels (Falge *et al.*, 2002b), minimum daily GPP in Puéchabon occurs during summer (data not shown), highlighting the fact that water availability, is, in absolute terms, the strongest limitation factor for ecosystem C fluxes in Puéchabon. This clearly points out water availability as the main determinant of NEP of forest ecosystems under Mediterranean climate. This clear water availability control over NEP is even detectable in submitted to a Mediterranean-type climate but at high elevation (>1000 m). These ecosystems located in the west part of the United States differs from European MTE because of their low winter temperature. Nevertheless, an annual NEP at those sites shows

Table 2 Site information (T, annual average temperature, R, annual rainfall) and yearly budgets of NEE submitted to a Mediterranean climate

Site	Country	T (°C)	R (mm)	Elevation (m)	Dominant species	NEE g C m ⁻² yr ⁻¹	Period	Reference
Puéchabon	France	13.5	907	270	<i>Quercus ilex</i>	-149 to -451	1998–2006	This study
Castelporziano	Italy	15.6	781	68	<i>Quercus ilex</i>	-547 to -598	1996–1999	Tirone <i>et al.</i> (2003)
Castelporziano	Italy	15.3	770	68	<i>Quercus ilex</i>	-660	1997	Valentini <i>et al.</i> (2000)
Arca di Noé	Italy	15.9	588	28	<i>Quercus ilex</i>	-70	1998–1999	Miglietta & Peressotti (1999)
Mitra	Portugal	15–16	669	220–250	<i>Quercus ilex</i> and <i>Quercus suber</i>	-140 to -28	2003–2006	Pereira <i>et al.</i> (2007)
Espira	Portugal	15–16	709	220–250	<i>Eucalyptus globulus</i>	-861 to -399	2003–2006	Pereira <i>et al.</i> (2007)
Yatir	Israel	18.2	270	650	<i>Pinus halepensis</i>	-130	2000–2001	Grunzweig <i>et al.</i> (2003)
Vaira ranch	CA/USA	16.5	562	129	<i>Quercus douglasii</i>	-115 to -56	2000–2006	Ma <i>et al.</i> (2007)
Blodgett	CA/USA	11.9	1473	1315	<i>Pinus ponderosa</i>	-339	1997–2000	Falge <i>et al.</i> (2002a, b)
Sky oak	CA/USA	12.2	491	1430	<i>Adenostoma sp.-Ceanothus sp.</i>	-67 to -60	1997–1999	Falge <i>et al.</i> (2002a, b)

NEE, net ecosystem exchange.

higher values in well-watered site than in low watered site (Table 2).

NEP variability in Mediterranean forest cannot be fully explained by the intensity of the summer drought. Because an important proportion of NEP is allocated to biomass increment in forest ecosystems, depending on the age of the stand, the intrinsic growth rate of the dominant species also largely affects NEP. Forests of fast growing species thus exhibit high NEP in absolute terms such as a plantation of *Eucalyptus* that fixed $-861 \text{ g C m}^{-2} \text{ yr}^{-1}$ in the wetter hydrological year of the study (Pereira *et al.*, 2007) or in comparative terms in regard with the annual rainfall of the site, such as a *Pinus halepensis* forest located at the edge of the Negev desert fix $-130 \text{ g C m}^{-2} \text{ yr}^{-1}$ despite an extremely low annual rainfall of 270 mm (Grunzweig *et al.*, 2003).

The 9 years dataset presented here allows refining the generic pattern described above. Indeed, more than the total annual rainfall, the rainfall occurring during the active growth period is a major determinant of NEP. A strong correlation can be found between the total rainfall occurring between March and June and NEP ($r^2 = 0.88$, $P = 0.006$; Fig. 4). This is supported by other studies in other Mediterranean ecosystems (Xu & Baldocchi, 2004; Pereira *et al.*, 2007). The amount of spring precipitation is the main factor determining sink CO_2 strength (Miglietta & Peressotti, 1999; Xu & Baldocchi, 2004; Ma *et al.*, 2007; Serrano-Ortiz *et al.*, 2007) since more than 80% of the yearly NEP occurs during these months (Fig. 2). As a conclusion, the interannual variability of NEP is significantly linked with the length of the growing season, the latter depending on the amount of seasonal precipitation. For example, an extremely dry spring occurred in 2006 and led to the lower recorded NEP in Puéchabon (Fig. 4). A similar effect was

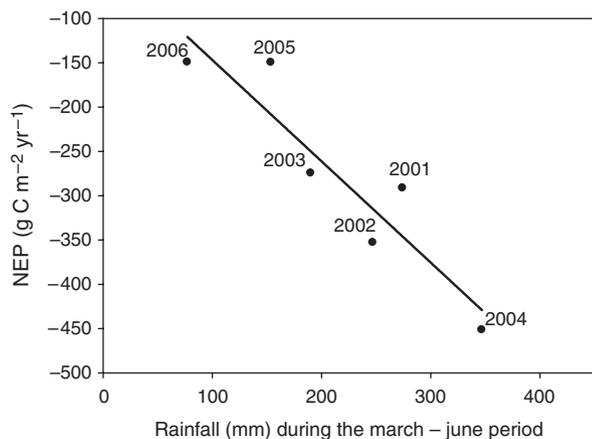


Fig. 4 Relation between ecosystem annual NEP sum for the six fully recorded years (2001–2006) and rainfall sum during spring (March–June). NEP, net ecosystem productivity.

observed in 2005 although part of the low NEP in that year can be explained by a caterpillar (*Limantria dispar* L.) attack during the spring of 2005. This additional stress explains the departure from the NEP/spring rainfall relation observed (Fig. 4).

Seasonality of ecosystem C fluxes: effects of environmental variables

The average seasonal course of ecosystem CO_2 flux at Puéchabon highlights the fact that both GPP and R_{eco} are under relatively simple controls when considered at the monthly integration level. We are aware that such a simple determinism is often inadequate to explore half-hourly flux data, in particular for R_{eco} (Papale *et al.*, 2006) but this is beyond the scope of the present paper. Outside of the dry season, GPP and R_{eco} can be satisfactorily described by simple statistical models (Fig. 3), with GPP following a classical hyperbolic relation to PAR (Fig. 3a) and R_{eco} a Q_{10} type function to soil temperature (Lavigne *et al.*, 1997; Law *et al.*, 2002; Reichstein *et al.*, 2002; Joffre *et al.*, 2003). Therefore, the dephasing of the PAR and soil temperature annual time courses (Fig. 2c) is the main determinant of the annual NEE pattern. During the first part of the year, PAR rapidly reaches near-optimal levels for GPP in spring but then decreases rapidly with the shortening day length in the autumn/winter. By contrast, the soil temperature time course reaches its maximum in summer and displays similar values in spring and autumn (Fig. 2c). This led to a relatively symmetric and bimodal distribution of R_{eco} (Fig. 2b) at the yearly level with a peak during the April–June period and a peak during the September–October period. The first peak of R_{eco} occurs during the growth season were the growth respiration component represent 13–37% of R_{eco} depending on the year (Rambal *et al.*, 2004). During the autumn peak, no growth respiration was detected and the major part of R_{eco} would be heterotrophic respiration promoted by high soil temperature and high soil water content. The dephasing between GPP and R_{eco} implies that 16% of the average annual NEP occurs between January and February and 82% between March and June (Fig. 2b). This clearly puts into perspective the advantage of evergreenness in environments characterized by relatively mild winters with air temperature that do not strongly limit the C acquisition process. Even if instantaneous photosynthesis in evergreen trees is often not maximized (Warren & Adams, 2004), leaf persistence allows a large amount of ecosystem productivity to be achieved during winter and spring.

During the summer months, when water availability is strongly limiting ecosystem functioning, both GPP and R_{eco} are drastically decreased (Fig. 2b). During

these periods, the best descriptor for ecosystem GPP is WSI, an integrated indicator of water stress (Fig. 3). From the relation $GPP = f(\text{PAR})$ in absence of water stress shown in Fig. 3, a theoretical optimal summer GPP can be calculated. Following this assumption, the difference between observed and calculated GPP showed that summer water stress induces a decrease of 200 g C m^{-2} , i.e. about 16% of the annual GPP. A similar detrimental effect of water stress on GPP was described for different Mediterranean ecosystems (Goldstein *et al.*, 2000; Law *et al.*, 2000; Rambal *et al.*, 2003; Xu & Baldocchi, 2004; Ma *et al.*, 2007; Pereira *et al.*, 2007). Reichstein *et al.* (2002) discussed the physiological basis for this negative effect of water stress on GPP. In particular, they hypothesized that drought-induced limitation of GPP includes more than classical stomatal limitation and list several phenomenon that may be responsible for this supplementary reduction of GPP including stomatal patchiness, decreased mesophyll CO₂ conductance (Roupsard *et al.*, 1996), and photoinhibition (Werner *et al.*, 1999).

The central role of soil moisture over R_{eco} has already been described for this site (Reichstein *et al.*, 2002; Joffre *et al.*, 2003) and is a constant in all Mediterranean ecosystems, whether forests (Law *et al.*, 2000) or grassland (Xu & Baldocchi, 2004). Our dataset shows that under water stress, the variable that explains the greatest part of R_{eco} variability is the topsoil relative water content rather than WSI (Fig. 3). Ecosystem respiration is indeed largely dominated by soil respiration whether autotrophic (roots) or heterotrophic (soil microorganisms) (Law *et al.*, 2001, 2002). In the stony Puéchabon soil, live roots and soil organic matter are mostly contained in the upper part of the soil profile (0–0.5 m). Therefore, if aboveground plant respiration is under a similar environmental control as GPP (i.e. a function of WSI), soil respiration is largely governed by the topsoil water status. This suggests that under limiting moisture conditions GPP and R_{eco} are partly decoupled, even if this phenomenon is hardly detectable at the monthly integration level used in this study. Nevertheless, it may partly explain the high variability of NEE during the summer months (Fig. 5). Such a phenomenon is a common characteristic of Mediterranean ecosystems. During the summer drought, when small rain episodes occur, the resulting short-term increase of topsoil water content allows a quick recovery of soil activity (Joffre *et al.*, 2003; Baldocchi & Valentini, 2004) and subsequently drives loss of C for the ecosystem. At 2 monthly scale, such events are not visible but a precise observation of daily R_{eco} data show this phenomenon (data not shown). These flush of R_{eco} occurred generally in September after a dry period, and had duration of 2–6 days and represent $15\text{--}93 \text{ g C m}^{-2}$ corresponding to

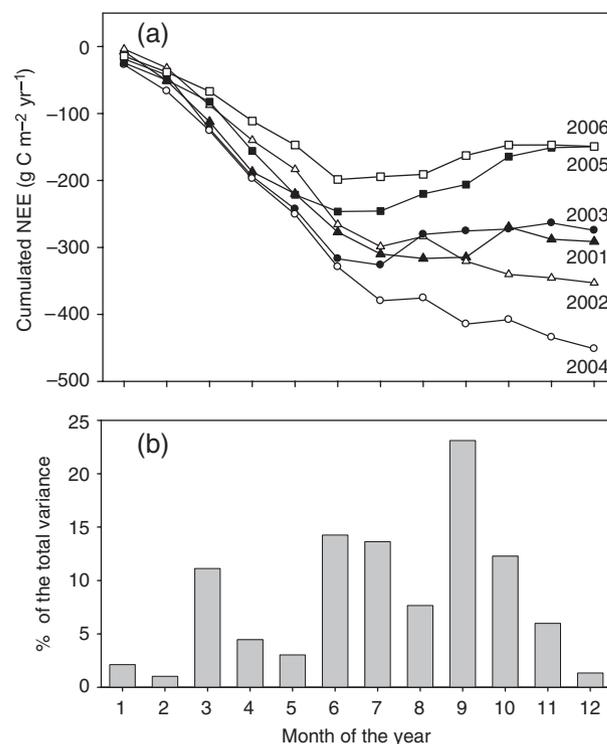


Fig. 5 (a) Cumulative NEE budget for the six fully recorded years (2001–2006) and (b) part of the total NEE variance attributed to each month. NEE, net ecosystem exchange.

3–9% of annual R_{eco} depending on the year. Nevertheless, the overall impact of such short-term events on the monthly and/or yearly ecosystem C budget is small at our site.

Possible impacts of climate change on the C budget of evergreen Mediterranean ecosystems

The Mediterranean area has been recently been pointed out as the most prominent climate change response region based on a study of climate-change induced variability of rainfall and air temperature (Giorgi, 2006). These predictions include a large decrease in April–September total rainfall (–22%) and increase in the associated variability (+40%). Comparatively, the rainfall deficit predicted for winter time is moderate (–10%; Giorgi, 2006). Based on the present study, it seems that the functional response of ecosystems to climate change is more important than the quantitative determination of climate change by itself. Indeed, in evergreen MTE, most of the growth occurs during the cool, wet spring (Archibold, 1995), a period for which climate variability in the past was moderate based on our observations. In the future, if the decrease of precipitation predicted for April to September (Giorgi,

2006) occurs during the first 3 months (spring), this can lead to a dramatic decrease of annual NEP. Oppositely, if the decrease occurs during the last 3 months (summer), the impact on annual NEP would be minimal.

Modified rainfall pattern under future climate should be considered in conjunction with other climate change components that may modulate possible detrimental effect of increasing water stress on Mediterranean ecosystem NEP. In particular, the rise of atmospheric CO₂ concentration has been identified as an important factor in Mediterranean ecosystems (Osborne *et al.*, 2000), mainly through the CO₂ driven raise of water use efficiency (Pan *et al.*, 1998). This phenomenon is potentially crucial in water-limited systems such as Mediterranean forest. Ecosystem NEP may also be stimulated if the predicted rise in air temperature during winter (Giorgi, 2006) occurs by increasing the GPP/*R*_{eco} differential already observed at this site (Fig. 2).

Another potential effect of climate change is suggested by our study: the indirect effects of climate change through insect herbivory on ecosystem C budget. The large decrease of annual NEP observed in 2005 (Fig. 5) due in part at the caterpillar defoliation shows the detrimental effect of a massive caterpillar attack on the ecosystem LAI. The stand LAI decreased of 5% to nearly 16% with a high spatial variability. Given this strong variability of, and the co-occurrence of, a spring in 2005, we could not quantify a direct effect of the defoliation on NEP. Higher temperatures under future climate, in particular in winter/spring may well increase the available thermal budget for growth and reproduction of insect herbivores (Bale *et al.*, 2002), and thus increase the herbivory pressure on the vegetation. Owing to the complex interactions between climate, vegetation and insect herbivores, prediction is difficult but some studies have shown an increase in the population size of some insect herbivores irrespective of the vegetation response (Masters *et al.*, 1998).

In addition, climate change may also profoundly alter soil functioning and subsequent exchange of CO₂ at the ecosystem/atmosphere interface. The fate of relatively stable C pools cannot be accounted for using the simple environmental drivers/C fluxes relations presented in this study. Interactions between climate change and fire frequency should also be accounted for (Mouillot *et al.*, 2002). Therefore, efforts in term of biogeochemical modeling and long-term monitoring of ecosystem C exchange are needed in order to predict future functioning of evergreen Mediterranean ecosystems.

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