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Annual variation in soil respiration and its components in a coppice oak forest in Central Italy

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Abstract

In order to investigate the annual variation of soil respiration and its components in relation to seasonal changes in soil temperature and soil moisture in a Mediterranean mixed oak forest ecosystem, we set up a series of experimental treatments in May 1999 where litter (no litter), roots (no roots, by trenching) or both were excluded from plots of 4 m^2. Subsequently, we measured soil respiration, soil temperature and soil moisture in each plot over a year after the forest was coppiced. The treatments did not significantly affect soil temperature or soil moisture measured over 0–10 cm depth.

Soil respiration varied markedly during the year with high rates in spring and autumn and low rates in summer, coinciding with summer drought, and in winter, with the lowest temperatures. Very high respiration rates, however, were observed during the summer immediately after rainfall events. The mean annual rate of soil respiration was 2.9 $\mu mol\ m^{-2}\ s^{-1}$, ranging from 1.35 to 7.03 $\mu mol\ m^{-2}\ s^{-1}$.

Soil respiration was highly correlated with temperature during winter and during spring and autumn whenever volumetric soil water content was above 20%. Below this threshold value, there was no correlation between soil respiration and soil temperature, but soil moisture was a good predictor of soil respiration. A simple empirical model that predicted soil respiration during the year, using both soil temperature and soil moisture accounted for more than 91% of the observed annual variation in soil respiration.

All the components of soil respiration followed a similar seasonal trend and were affected by summer drought. The Q_{10} value for soil respiration was 2.32, which is in agreement with other studies in forest ecosystems. However, we found a Q_{10} value for root respiration of 2.20, which is lower than recent values reported for forest sites. The fact that the seasonal variation in root growth with temperature in Mediterranean ecosystems differs from that in temperate regions may explain this difference. In temperate regions, increases in size of root populations during the growing season, coinciding with high temperatures, may yield higher apparent Q_{10} values than in Mediterranean regions where root growth is suppressed by summer drought.

The decomposition of organic matter and belowground litter were the major components of soil respiration, accounting for almost 55% of the total soil respiration flux. This proportion is higher than has been reported for mature boreal and temperate forest and is probably the result of a short-term C loss following recent logging at the site.

The relationship proposed for soil respiration with soil temperature and soil moisture is useful for understanding and predicting potential changes in Mediterranean forest ecosystems in response to forest management and climate change.

Keywords: litter and SOM decomposition, Mediterranean oak forest, root respiration, soil moisture and soil temperature, soil respiration

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Introduction

Soil respiration provides the main carbon efflux from ecosystems to the atmosphere and is therefore an important component of the global carbon balance (Schimel, 1995). Rates of soil respiration are known to be highly sensitive to soil temperature and moisture content and thus a future warmer climate may increase the flux of CO_2 from the soil (Jenkinson *et al*., 1991). Recent global circulation models include potential increases in atmospheric CO_2 concentration and temperature (e.g. Cox *et al*., 2000), and changes in the distribution of precipitation and evaporation (Mitchell *et al*., 1999; Cooter *et al*., 2000; Dai *et al*., 2001). Despite current uncertainties in predicting changes in rainfall patterns, there are clear indications that several arid and semiarid regions will experience larger water deficits than at present, resulting not only from smaller annual amounts of precipitation but also from changes in rainfall distribution (Ramball & Debussche, 1995).

As a result of climate change, and the increasingly recognized importance of the role of soils now and in the future, more efforts are being put into making better estimates of soil CO_2 efflux and to improve our understanding of the interactions between environmental variables and soil respiration. However, soil processes in ecosystems exposed to drought, and in Mediterranean ecosystems in particular, have received much less attention (Raich & Schlesinger, 1992; West *et al*., 1994; Raich & Potter, 1995). Although these ecosystems may not be so relevant in terms of the amount of C stored in them, they occupy one third of the land surface of the earth (Emanuel *et al*., 1985) and are highly vulnerable to climate change (West *et al*., 1994).

So far, most long-term global modelling studies have included soil temperature as the sole variable determining soil respiration. However, annual soil respiration fluxes in Mediterranean ecosystems, and in semiarid ecosystems in general, are highly sensitive to soil moisture (Amundson *et al*., 1989; Kaye & Hart, 1998), so that soil temperature alone is clearly insufficient to predict soil respiration. Several studies have concluded that decomposition will increase more rapidly than production in many ecosystems, resulting in a net decrease in soil organic carbon (C) and increase in atmospheric CO_2 concentration (e.g. Thornley *et al*., 1991; Schimel, 1995; Cramer *et al*., 2001). Extensive analyses of soil C stocks in relation to climate have found positive correlations between soil organic C stocks and precipitation, and, at a given precipitation, negative correlations with temperature (e.g. Post *et al*., 1985). Other studies have shown that in semiarid ecosystems soil respiration increases with both C pool size and mean annual precipitation, but decreases with increase in mean annual temperature (e.g. Conant *et al*., 1998).

Soil CO_2 efflux is the result of autotrophic respiration by roots and associated mycorrhizae, and heterotrophic respiration by microorganisms and soil fauna that decompose aboveground litter and belowground detritus and soil organic matter. Despite the growing body of information on soil respiration processes, partitioning between autotrophic and heterotrophic respiration remains clearly unresolved and the issue of how different components of soil respiration are likely to respond to climate change is highly controversial (e.g. Kirschbaum, 1995; Trumbore *et al*., 1996; Giardina & Ryan, 2000).

Gross primary production (GPP) is yet another factor influencing soil respiration since it provides the inputs to the soil of aboveground litter and belowground organic detritus. Analysis of NEE data from the EUROFLUX forest sites showed no significant correlation between annual ecosystem respiration and temperature across Europe but, instead, a correlation with GPP (Janssens *et al*., 2001). Any changes in the inputs of litter and detritus to the soil as a result of forest management or climate change, in addition to any changes in temperature and moisture content, are likely to affect rates of soil respiration strongly and to influence the contribution of the different components to the total respiratory CO_2 efflux from the soil. Although forests in Europe are rarely natural and most of them are managed to varying degrees, studies on belowground processes in managed forests are very scarce.

Partitioning the soil CO_2 efflux between autotrophic and heterotrophic respiration has proved difficult. The different methods and approaches used have been recently reviewed by Hanson *et al*. (2000). Early attempts were made by removing roots from the soil in the laboratory (e.g. Wiant, 1967), or by measuring the respiration of roots *in situ* directly after removing the soil around them (e.g. Edwards & Sollins, 1973). Estimates have also been made by finding a relationship between soil respiration and fine root biomass using simple regression analysis (Kucera & Kirkham, 1971; Xu *et al*., 2001). Other attempts have consisted of digging trenches around small areas to exclude roots and hence to eliminate root growth and respiration (e.g. Bowden *et al*., 1993; Boone *et al*., 1998; Epron *et al*., 1999a). More recently isotopic approaches have been developed in which the isotopic signal of the soil CO_2 efflux has been used to derive the partitioning (Hanson *et al*., 2000). Although such methods have clear advantages because of the lack of soil and root disturbance, the high costs and complexity of the analyses have limited their use to a few situations in boreal forest (Trumbore *et al*., 1996; Ekblad & Högberg, 2001) and elevated CO_2 studies (Lin *et al*., 1999). Very recently, a novel estimation of the root contribution to total soil respiration of Scots pine has been made in a large-scale girdling experiment in which the phloem was cut away

on 720 trees, in a fully replicated design, while the xylem continued to allow water movement (Högberg *et al*., 2001). These different methods all have intrinsic limitations associated with either the sampling methodology or changes in soil conditions as a consequence of the absence of living roots and increased input of root detritus to the soil, and have yielded estimates of root respiration ranging from 10 to 90% of the total (Hanson *et al*., 2000).

We initiated a combination of laboratory and field studies to elucidate the response of soil respiration to temperature and moisture in both controlled and field conditions in a Mediterranean oak forest. In this paper, we present field-based data on the annual variation of soil respiration in a combination of treatments comprising root and litter exclusion plots through the first year of the experiment. Our specific aims were: (1) to evaluate the seasonal variation of soil respiration and its components in a coppiced-oak, Mediterranean forest; (2) to evaluate the relative importance of soil temperature and soil moisture as predictors of soil respiration; and (3) to estimate the relative contributions of root respiration, aboveground litter and soil organic matter (SOM) decomposition to the total soil CO_2 efflux.

Materials and methods

Site description

The experimental site is situated in the forest of Roccarespampani in the Comune di Monteromano (Lazio, province of Rome) in the basin of the river Marta (coordinates 42°24′N and 11°55′E). The forest occupies around 1250 ha in a fairly flat area varying from 120 to 160 m above sea level. The phytoclimatic zone is Lauretum. The precipitation regime is characterized by irregular distribution of rainfall with a summer drought period of about two months. The mean annual precipitation is 755 mm and temperature 14 °C (Table 1).

The forest is a coppice of *Quercus cerris* L. with a rotation length of 15–20 years between coppicing. Other species such as *Quercus petraea* (Matt.) Liebl., *Quercus pubescens* Willd. are present, and to a lesser extent *Quercus suber* L., *Quercus ilex* L., *Quercus robur* L., *Carpinus betulus* L., and *Juniperus communis* L., as well as other shrub species typical of the Mediterranean macchia in the understorey layer, such as *Prunus spinosa* L., *Ruscus aculeatus* L., and *Colutea arborescens* L.

The geological substrate is derived from sedimentary material of volcanic origin and marine deposits. The soil is characterized by the presence of crystallized clay particles with a sandy clay texture. Soil depth is *ca.* 1 m. Most root systems penetrate to a depth of 50 cm with the highest root density in the top 20 cm. The area comprises 15 compartments that have been managed as coppice over the last 200 years. Before that there was an intact forest dominated by *Quercus cerris*. Coppicing consists of selective logging of trees in each compartment leaving intact trees of *ca.* 30 cm in diameter about every 10 m. The trees are kept for about three coppice rotations so that the oldest trees in the plots are around 45 years old. The compartments are consecutively coppiced approximately every 20 years. The result is a mosaic of compartments of different age-stands ranging from 0 to 20 years after coppicing. This study is focused on a compartment of about 100 ha that was logged in January 2000.

The site was one of the European MEDEFLU network of sites during 1998–99 and is currently a site of the European projects CARBOEUROFLUX, CARBOAGE and FORCAST. In the compartment, an eddy covariance system has been running since 1998 measuring fluxes of CO_2 and H_2O vapour. We took advantage of the logging activity to evaluate the contribution of the different components of soil respiration after coppicing.

Table 1 Main characteristics of the field site of Roccarespampani (Province of Lazio)

Variable	
Main characteristics	
Main Species	*Quercus cerris*
Longitude	11°55′E
Latitude	42°24′N
Area (ha)	1250
Elevation (m)	120–160
Average annual temperature (°C)	14
Average annual rainfall (mm)	755
Stand characteristics	
Standing biomass (tonne ha^{-1})	32,1
Leaf area index (m^2 m^{-2})	1.40
Tree diameter (cm)	4.9
Tree density (ha^{-1})	745
Tree height (m)	15
Amount of woody debris (tonne ha^{-1})	24
Litter fall (g m^{-2})	75.6
Rotation length ($year^{-1}$)	15–20
Soil characteristics	
Soil type	Luvisol
Soil mineralogical class	Volcanic
Soil depth (cm)	100
Root depth (cm)	50
Ph	5.7
C/N	12.6
Bulk density (kg ha^{-1})	1.22
Fine root biomass (< 2 mm) 0–45 cm (kg m^{-2})	0.95
% sand	52
% silt	12
% clay	35

Experimental design

In May 1999 six trees of approximately 50 cm in diameter and 25 m in height distributed through the compartment were selected and six experimental areas each consisting of four treatment plots were set up around each tree. Each experimental block (7×7 m) was surrounded with 1 m tall fence. At about 2 m from the trunk of each tree, 2×2 m plots, free of trees or shrubs, were marked out in four directions, and the following treatments were applied at random: control [C] (undisturbed), no-litter [NL] (aboveground litter excluded), no-roots [NR] (root growth excluded) and no-litter-no-roots [NLNR] (both litter removed and roots excluded). Existing litter was removed and litterfall was excluded by placing litter traps made of garden netting over the NL and NLNR plots during the autumn (from late October before litterfall through to the end of January when all leaves had fallen). Roots were excluded from the NR and NLNR plots by trenching 1-m deep trenches (20 cm wide) and installing fibreglass sheets to prevent root entry. The trenches were back-filled with the same soil. Trenching was done with maximum care to minimize soil disturbance to the plots that remained untrenched. To allow decomposition of the roots within the plot, we left the area to recover for eight months until February 2000, when measurements started. We monitored soil respiration inside the trenched plots during this time until stable rates were observed. We assumed that the contribution of the remaining fine and coarse roots to the total soil respiratory flux was small. From the beginning, and throughout the course of the experiment, the plots were maintained free of seedlings and herbaceous vegetation. In January 2000, the entire compartment was logged leaving trees spaced at *c.* 10 m. Large amounts of woody debris were left on the forest floor after the logging, and have been quantified.

Temperature and moisture measurements

Soil temperature was monitored with temperature probes installed in two plots of each treatment (i.e. a total of eight) in November 1999 (T107, Campbell Scientific Ltd. Loughborough, UK) that were inserted vertically to a depth of 10 cm into the mineral soil. The sensors were connected to a datalogger (Model CR10, Campbell Scientific Instrument Ltd) set to record 15 min average values hourly. In addition, soil temperature and soil moisture were measured with portable sensors: a STP-1 probe (PP-Systems Ltd. Herts, UK), and a Theta probe (ML2x, Delta-T Devices Ltd, Cambridge, UK), respectively, inserted adjacent to the soil collars at the time of each soil respiration measurement. During the summer months (i.e. July through September) the soil became very dry and hard and consequently it was not possible to insert the portable sensors into the ground. We took soil samples from the first 10 cm of soil and determined soil moisture content gravimetrically by oven-drying the soil at 105 °C for 24 h. A conversion using bulk density was used and the data were corrected accordingly ($R^2 > 0.99$). For the soil temperature, we established a regression between the permanent sensors and the STP-1 probe ($R^2 > 0.95$), so that adjusted data from the permanent sensors could be used.

Soil respiration measurements

Two soil collars made of PVC, 10 cm in diameter and 4.5 cm long, were inserted 2.5 cm into the soil in each plot (total of 48 points) in January 2000. Once inserted, the collars were left in place throughout the course of the experiment. Soil respiration (SR) was measured regularly (between one and four times a month depending on the season) with a portable, closed, dynamic chamber (EGM-2 with SRC-1, PP-Systems, UK) slightly modified to fit the soil collars with a perfect seal. Measurements were always made between 9.00 a.m. and 1.00 p.m. to avoid diurnal fluctuations. The average value of the two measurements per plot was used for data analysis. The average soil temperature and soil moisture recorded next to each measuring collar at two locations at the time of SR measurements were also used in this analysis.

To examine whether the SR rates measured in each treatment were consistently different over time and whether application of the treatments had significantly affected soil environmental conditions in the plots, SR, soil temperature and soil moisture data were analysed using a two-way ANOVA with repeated measures analyses on one factor (Sokal & Rohlf, 1995). A further LSD multicomparison test was used to reveal differences between treatments. All data analyses were performed using SAS statistical software (SAS Institute, USA).

Litter inputs

The amount of coarse woody debris (CWD) left after the logging was quantified by selecting two parallel transects of approximately 100 m length within the compartment. CWD was collected from sample plots of 1 by 1 m every 10 m along the transects. All woody material was collected, weighed and a subsample from each sample plot, oven-dried at 80 °C until constant mass and reweighed. Annual leaf litterfall was quantified with litter traps of 50 cm in diameter and 1 m long located at random in the compartment ($n = 25$). In February 2000, after all leaves had fallen, all litter from each litter trap was removed, weighed and a subsample was dried at 80 °C for dry mass determination.

Modelling annual soil respiration

The following exponential function was used to describe the *temperature dependence of SR* in each treatment:

$$R = R_0\ e^{\beta T}$$

Where R is the measured soil respiration ($\mu mol\, m^{-2}\, s^{-1}$), R_0 is the basal respiration at temperature of 0 °C, T is soil temperature over 0–10 cm (°C) and β is the temperature coefficient, which is related to the Q_{10} (increase in the rate of respiration over a 10 °X increase in temperature) as follows:

$$\frac{R_{T+10}}{R} = Q_{10} = e^{10\beta}$$

The use of this first-order exponential model has been criticized for not taking into account the change of Q_{10} with temperature (Lloyd & Taylor, 1994) and thus producing a single value of Q_{10} independent of the temperature range over which respiration was measured. For this reason we also used the Arrhenius equation, which has been suggested as a better function because of its theoretical basis (Lloyd & Taylor, 1994; Fang & Moncrieff, 2001). This did not, however, improve the estimates in our case and consequently we do not present the parameterization here. Soil respiration was related to temperature when the volumetric soil water content was above 20%, so only these data were used to fit the relationship (Proc NLIN).

A linear function was used to describe the relationship between *soil respiration and soil water content* over 0–10 cm. SR was related to soil moisture when soil moisture was below the 20% volumetric water content, which largely occurred in the summer. These data obtained in the summer after rainfall events were used to fit the relationship (Proc REG). The choice of the form of the relationships was based on the simplest statistical model that explained most of the variance. Based on these equations we put together an empirical model to predict SR using both soil temperature and soil moisture over 0–10 cm as driving variables.

Contribution of aboveground litter decomposition, root respiration and SOM decomposition to SR

The contributions of the different components to the total respiratory flux were estimated by comparing the soil CO_2 efflux in the various treatments. The respiration measured in the control plots (R) was the result of the following processes: aboveground litter decomposition (R_L), rhizosphere respiration (root, mycorrhizal and rhizosphere microbial respiration) (R_R), and the respiration resulting from the decomposition of SOM and fine root turnover (R_{SOM}). The respiration of the NL and NR plots enabled estimation of the contribution of R_L and R_R, respectively, as the difference from the total respiratory flux measured in the control plots: the respiration measured in the NLNR is the sole result of decomposition of the SOM (R_{SOM}). The contribution of each component was calculated for each day of measurements using the mean of all six replicated plots.

Results

Annual variation in soil temperature and soil moisture

Both soil temperature and soil moisture content varied markedly with season. Maximum temperatures coincided with minimum water contents in the summer and minimum temperatures were recorded in winter when soil moisture was highest (Fig. 1). Soil temperature increased steadily until mid-summer reaching a mean maximum in August of 27.8 °C (day 237) and then declined smoothly through autumn and winter until it reached the lowest value of 4.8 °C (day 359). The annual mean daily temperature of the soil was 15.6 °C. There was good agreement between soil temperature measured with the thermistors and with the SRC2 probe ($R^2 > 95$, slope = 1.0082, $P > 0.001$). Morning temperatures (measured at the same time as the SR measurements) followed the same trend with a minimum value of 7.0 °C recorded in February when these measurements started (day 53) and a maximum of 31.3 °C recorded in August (day 229) (Fig. 1).

No differences in mean daily temperature between treatments or in soil temperature over 0–10 cm measured in the morning ($P > 0.05$) were observed and soil temperatures were the same in all treatments for most of the year (Fig. 1). However, during the summer months (July and August) those treatment plots from which litter was removed tended to have higher soil temperatures in the morning than the control plots (average 24, 25.7 and 25.2 °C for the C, NL and NLNR treatments, respectively) and this was also observed to a lesser extent in the treatment from which roots were excluded (average 24.3 °C for the NR treatment).

Soil volumetric water content over 0–10 cm depth in the control treatment ranged from 51.7% in winter (day 363) to 6.08% in mid summer (day 242) with an average annual value of 28.8%. Soil water content was below 20% from June until the beginning of September, except after rain when it increased sharply. Treatments did not significantly affect soil water content ($P > 0.05$), but there was a tendency for it to be somewhat higher in the NR treatment because of the absence of root water uptake.

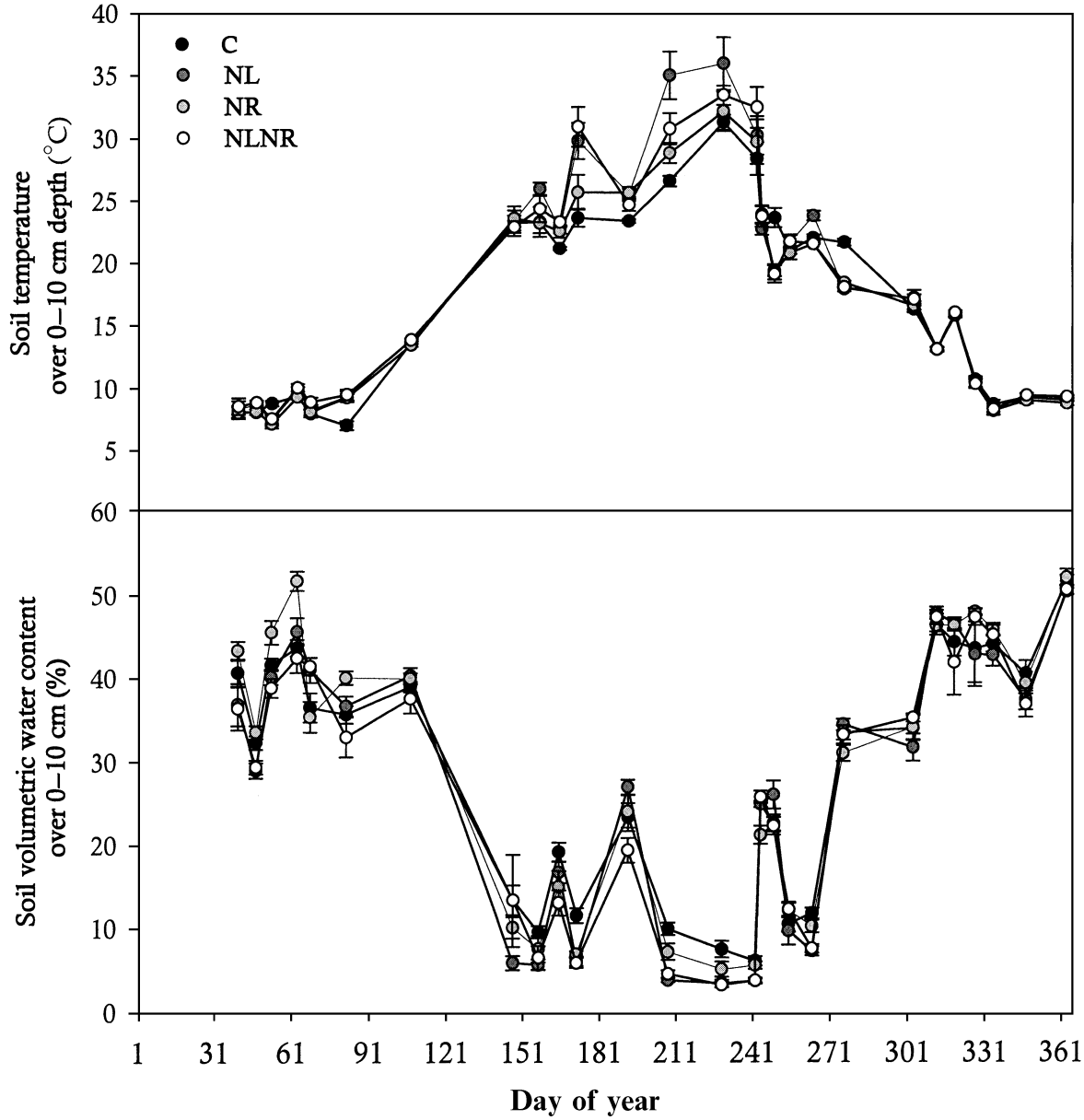

Fig. 1 Annual course of soil temperature and soil volumetric water content measured over 0–10 cm (with STP-1 probe and Theta probe, respectively) at the time of soil respiration measurements (between 9.00 and 13.00 h) in all the treatments ($n = 6$, mean $\pm$ SE): control (C), no-litter (NL), no-roots (NR) and no-litter-no-roots (NLNR) during the year 2000.

Annual litter inputs

The measured amount of aboveground litterfall during 2000 was 75.6 g m^{-2} ($\pm$ 5.76, $n = 25$), almost one fourth of the annual litterfall before the forest was coppiced. The amount of woody debris left on the forest floor during 2000 was 2.4 kg m^{-2} ($\pm$ 0.3, $n = 10$).

Annual variation in soil respiration

Soil respiration varied markedly during the year following the changes in soil temperature during the winter and part of the spring and autumn and the changes in soil moisture for the rest of the year (Fig. 2). Soil respiration increased steadily during spring following the

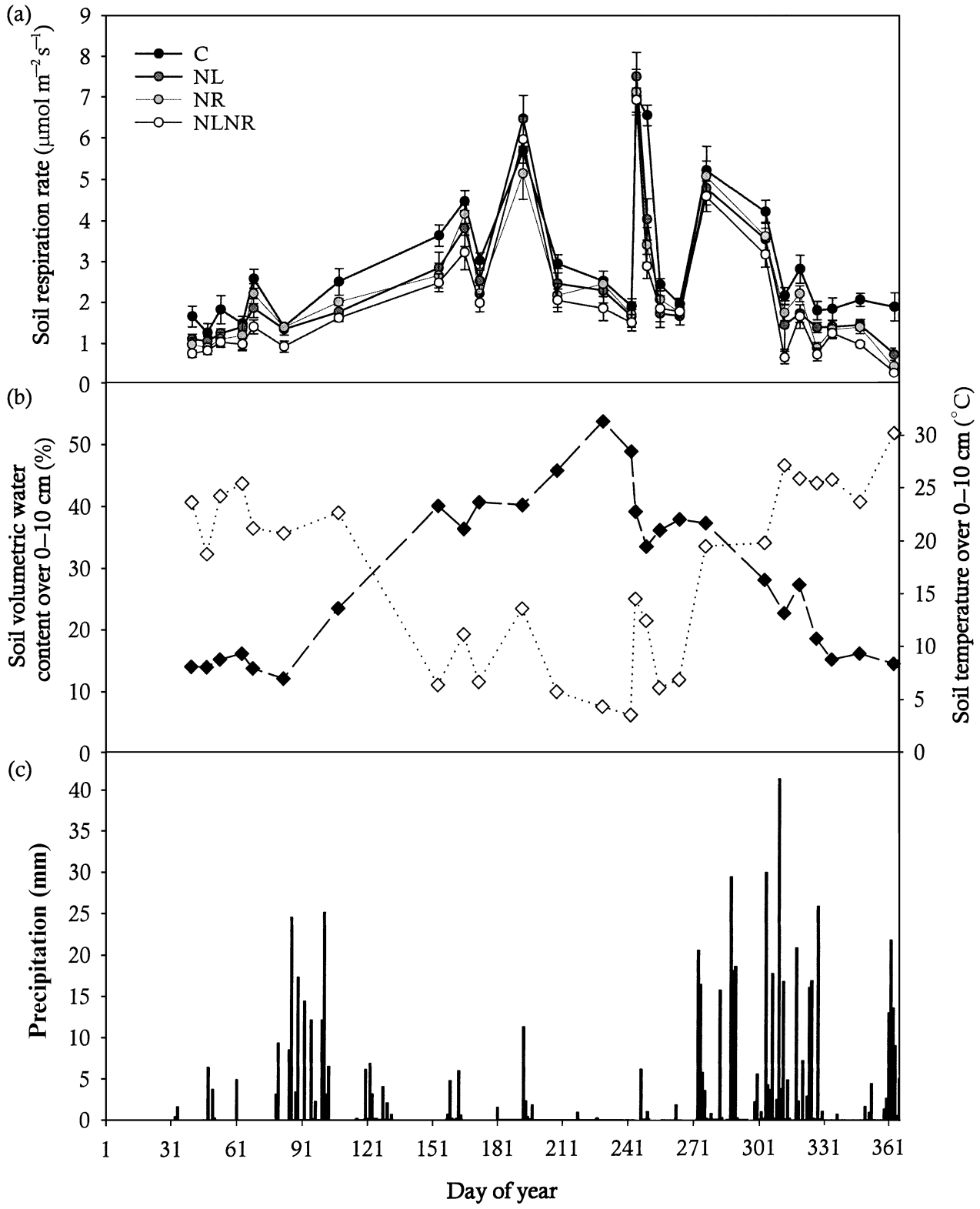

Fig. 2 Annual course of soil respiration (μmol m^{-2} s^{-1}) measured in the four treatments: control (C), no-litter (NL), no-roots (NR) and no-litter-no-roots (NLNR): (a) soil temperature and soil volumetric water content measured over 0–10 cm in the C treatment; (b) and daily precipitation (mm); (c) during the year 2000. Values in (a) are the mean (± SE) ($n = 6$).

increases in temperature until June when it reached a peak of 3.62 μmol $m^{-2} s^{-1}$. SR then declined in general during the dry summer months, although increasing sharply with rainfall events, before declining from a maximum value of 5.6 μmol $m^{-2} s^{-1}$ in September (day 236) to a minimum of 1.69 μmol $m^{-2} s^{-1}$ in winter (day 363). The effect of summer drought became apparent as soil water content fell below 20%. The limiting effect of soil moisture on soil respiration was clear as SR responded quickly and sharply to each rain event reaching its highest values (up to 7.02 μmol $m^{-2} s^{-1}$ on day 249) and then decreased to pre-rain values (Fig. 2).

As expected, SR rates were lowest over the winter when soil water contents were highest and soil temperatures lowest. This annual variation was the same in all treatments (Fig. 2) except for those days on which it rained when SR was more responsive in the NLNR treatment than in the other treatments. Repeated measures analyses of variance revealed significant differences between treatments ($P < 0.001$) with no significant interaction between time and treatments ($P > 0.05$), as differences between treatments were consistent throughout the year. A multi-comparison test revealed that the control treatment was significantly different from the others on most occasions. The average SR rates measured in each treatment were 2.90, 2.36, 2.31 and 2.00 μmol $m^{-2} s^{-1}$ for the C, NL, NR and NLNR treatments, respectively.

Contribution of aboveground litter decomposition, root respiration and SOM decomposition to total SR

The contribution of root respiration and litter decomposition to the total SR was calculated by subtracting SR rates measured in the NR and NL treatments from the rates measured in the C treatment. Data were averaged for each degree of temperature because the regression analyses failed the constant variance test as there were many more measurements at low temperatures than at high temperatures. This did not substantially change the goodness of the fit but avoided violation of the assumption. The Q_{10} values for R (whole system respiration), R_L (aboveground litter decomposition), R_R (root respiration) and R_{SOM} (belowground detritus and SOM decomposition) were 2.32, 3.48, 2.20 and 2.89, respectively (Table 2).

To ensure that the treatments worked in the expected manner, we compared the SR rates measured in the control plots with the rates calculated as the sum of the rates of the three components: i.e. litter decomposition (C – NL), root respiration (C – NR) and belowground decomposition (C – NLNR). The agreement was very good ($R^2 = 0.93$, slope close to 1) (Fig. 3).

To estimate the annual contribution of aboveground litter, root respiration and SOM (including belowground detritus) to the total respiratory flux during the year, we divided the year into seasons: winter (up to day 80), spring (day 81–172), summer (day 173–264) and autumn (day 265–365) and calculated the weighed average percentage contribution of the components during these periods (Fig. 4). The overall annual average was: 21.9, 23.3 and 54.8% for aboveground litter respiration, root respiration and belowground SOM and detritus decomposition, respectively. The contribution of aboveground litter to total SR was larger in spring and autumn than in the summer, coinciding with litterfall at the site (which started in late November and finished in January). The contribution of root respiration decreased over the year and was largest in autumn prior to leaf litterfall (the average daily temperature for this period was 8 °C).

Table 2 Parameters of the exponential relationship between soil respiration rate (μmol $m^{-2} s^{-1}$) and temperature (°C) ($SR = a * e^{(bT)}$) (a) and, of the linear relationship between soil respiration rate and soil moisture (%) ($SR = c * \rho + d$) (b) for the different soil processes: control (total soil respiration as measured in the C plots), aboveground litter decomposition (calculated from the difference between the C and the NL treatments), root respiration (calculated as the difference between the C and the NR treatment) and soil organic matter and belowground detritus decomposition (as measured in the NLNR treatment). Mean values per degree of temperature and moisture for the data from the six blocks were used. Values are the estimated parameters ± standard error (* = significant at 5%)

(a) Treatment	a	b	P	R^2	Q_{10}
Control	0.87* ± 0.09	0.08* ± 0.01	0.001	0.94	2.32 ± 1.04
Roots	0.49 ± 0.10	0.07* ± 0.02	0.001	0.52	2.20 ± 1.25
Litter	0.25 ± 0.09	0.13* ± 0.03	0.002	0.66	3.48 ± 1.38
SOM	0.39 ± 0.12	0.11* ± 0.01	0.001	0.84	2.89 ± 1.14
(b) Treatment	c	d	P	R^2	
Control	0.22* ± 0.03	0.79* ± 0.35	0.001	0.84	
Roots	0.08* ± 0.02	− 0.12 ± 0.32	0.016	0.49	
Litter	0.13* ± 0.02	− 0.22 ± 0.33	0.001	0.67	
SOM	0.18* ± 0.03	0.86* ± 0.40	0.001	0.68	

Response to soil temperature and soil moisture as predicative variables of soil respiration

Soil respiration was related to soil temperature over 0–10 cm for values of soil volumetric water contents higher than 20% (as shown in Fig. 5), but below this value there was no correlation. The parameters for the relationship between soil temperature and SR for each treatment using the first-order exponential are given in Table 2. Although the Arrhenius function described the relationship very well, the simpler exponential equation yielded higher R^2 values with the residuals equally distributed across the range of temperature measurements and was therefore preferred. Soil temperature accounted for 85% of the variation in SR above the threshold value of 20% soil water content.

For values of soil water content below 20% and for those above 20% measured in the summer after rainfall events (from day 157–264), SR measured in the control plot and soil moisture were positively correlated, although the relationship was not as good as with temperature (Fig. 5). Using average values per degree of moisture we obtained significant relationships between soil volumetric water content and SR over the summer months for all treatments. The parameters for the linear relationship between soil moisture and SR for each are given in Table 2.

Using the threshold value of 20% volumetric water content, we developed a simple empirical model using soil temperature and soil moisture down to 10 cm to predict soil respiration. Above this value soil temperature controlled soil respiration following an exponential function and below this value, soil respiration was linearly controlled by soil water content down to 10 cm (Fig. 6). Agreement between measured SR and soil respiration modelled in this way was very good, explaining more than 91% of the temporal variation in SR in the control plots.

To estimate quantitatively the effect of drought on SR, we compared predicted values of soil respiration, that are likely to have resulted if temperature had been the sole limitation of SR, with the values of SR actually measured

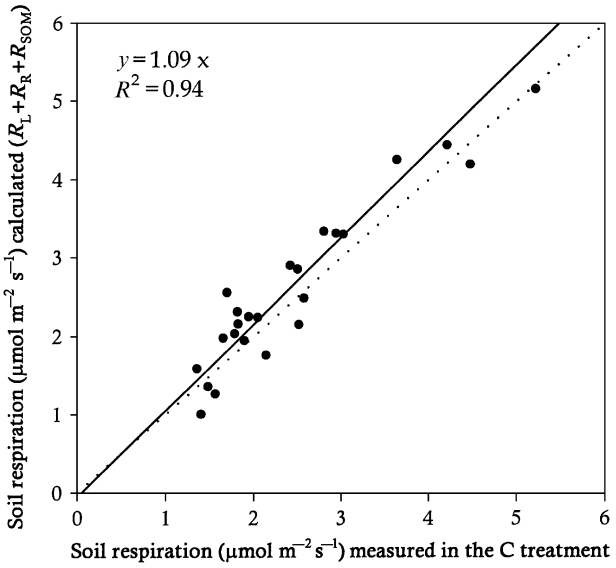

Fig. 3 Relationship between soil respiration measured in the control treatment and the calculated soil respiration as the sum of the different processes involved aboveground litter decomposition (*L*), root respiration (*R*) and belowground decomposition (SOM). The dotted line represents the 1 to 1 line. Values are the averages of six plots per treatment measured on each individual date.

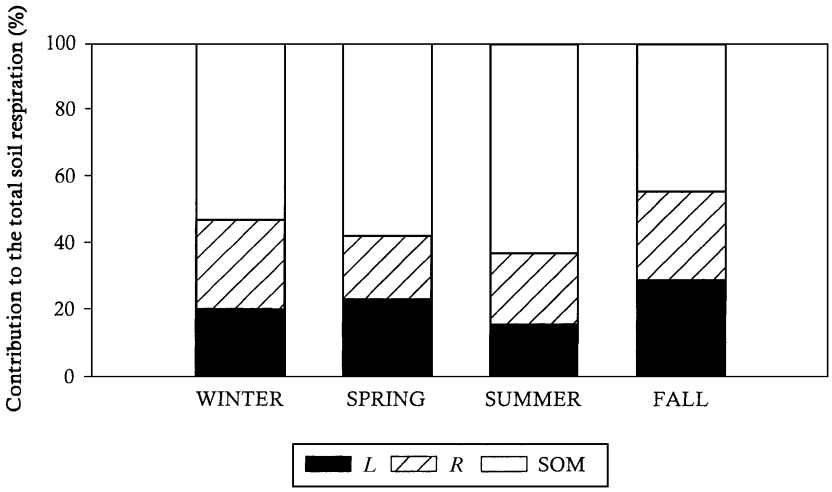

Fig. 4 Relative contribution of aboveground litter (*L*), root respiration (*R*) and belowground decomposition (SOM) to the total soil respiration (SR) over the year 2000 in four seasons: winter (up to day 80), spring (to day 172), summer (to day 264), and autumn (to day 365).

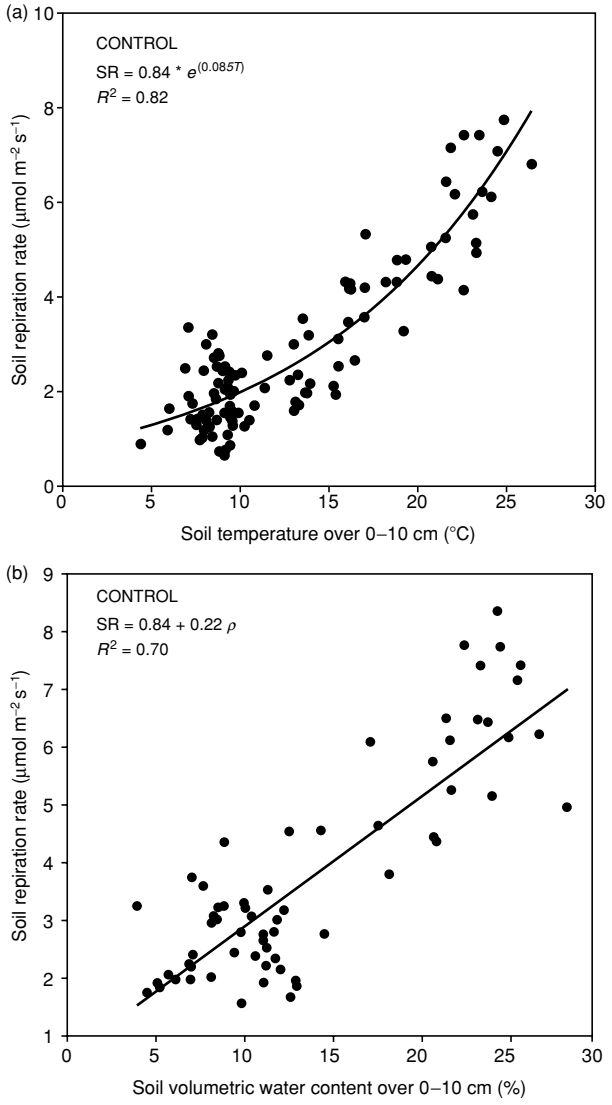

Fig. 5 The relationship between soil respiration rate ($\mu mol\,m^{-2}\,s^{-1}$) and soil temperature (°C) whenever soil volumetric water content was above 20% (a) and, soil volumetric water content (%) during the summer (from day 157 to day 264) (b) in the control plots. Individual values represent the mean of two measurements taken in each plot.

in the control plots (Fig. 6). From the discrepancy, we estimate that the annual reduction in SR as a result of soil moisture limitation was 37.4%. In order to obtain an approximate annual estimate of the total amount of C released at the site by SR, we assumed that the morning measurements were approximately the daily means. Then, we interpolated between sampling dates to estimate the mean flux each day of the year and added up all values to calculate the total for the year 2000 (except January). We obtained a total of $9.04\,Mg\,C\,ha^{-1}$.

Discussion

The range of soil respiration rates measured over the year in this study is similar to the range measured in other studies (e.g. Davidson *et al*., 1998; Law *et al*., 1999; Xu & Qi, 2001). Similar seasonal trends in soil respiration have also been observed elsewhere (e.g. Conant *et al*., 2000; Xu & Qi, 2001) and are characteristic of drought-stressed regions.

Effect of soil temperature on soil respiration

In agreement with other studies carried out in the Mediterranean region (e.g. Matteucci *et al*., 2000), the seasonal pattern of SR in the Roccarespampani forest followed soil temperature for only part of the year (winter and part of spring and autumn). Our Q_{10} for SR is in agreement with the median Q_{10} value for SR in forest soils of 2.4, although the variance around this value is large (Raich & Schlesinger, 1992; Kirschbaum, 1995). Other studies have reported higher Q_{10} values for SR. For example, Davidson *et al*. (1998) found Q_{10} values of 3.4 and 5.6, much higher than the values found in our study. They attributed this high value to the important contribution of roots to SR. Pretgitzer *et al*. (2000) reported a range of Q_{10} for root respiration of between 1.5 and 3. Lower values have been reported in other studies, such as the value of 1.8 found by Xu & Qi (2001) in a ponderosa pine forest in Northern California.

Respiration of both microbial communities and plant roots is sensitive to changes in soil temperature. We detected significant differences in the sensitivity of the different respiring communities involved in SR. The decomposition of aboveground litter and belowground detritus and SOM had significant, slightly higher Q_{10} than root respiration. This contrasts with previous studies that have found a higher Q_{10} for root respiration, than for SOM decomposition (Boone *et al*., 1998; Epron *et al*., 1999a). However, those studies were carried out in forests where moisture was not limiting and where soil temperatures were generally lower than at our site. It is possible that the high Q_{10} for root respiration observed in those experiments was not solely the result of higher sensitivity of *specific activity* of roots ($\mu mol\ CO_2\,g^{-1}$ root) to soil temperature, but was also in part the result of higher root densities during the summer. In drought-prone Mediterranean regions, seasonal variation in size of population of roots with respect to temperature differs from that in temperate zones, where higher population densities occur in the summer coinciding with the highest temperatures.

When a Q_{10} is calculated from a sequence of measurements taken over a period of time during which the temperature is changing, the resulting value may well

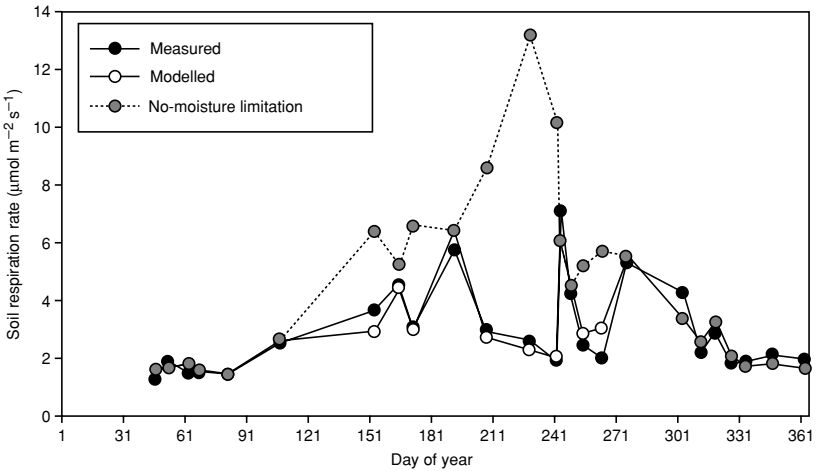

Fig. 6 Measured (●) (mean of 6) and modelled (○) soil respiration over the year 2000 in the control plots. The model is a simple empirical model where soil respiration rate is controlled solely by soil temperature whenever soil volumetric content was above 20% following a first exponential curve, and otherwise by soil moisture following a simple regression. Calculated soil respiration (SR) assuming no moisture limitation (◎) using a first-exponential curve to describe the dependence of soil respiration (SR) on soil temperature over 0–10 cm.

be the *product* of the response of the respiratory process itself to temperature and the response of the population of respiring organisms, whether fine roots or microorganisms, to temperature. During the spring, for example, when the temperature is increasing, both the specific rate of respiration *per se* and the sizes of populations of the respiring organisms are also increasing. If both processes have a Q_{10} of 2, the resulting measured Q_{10} would be 4. Respiration is a relatively conservative process with a well-established Q_{10} in the region of 1.8–2.4, so that variation from this range is most likely to result either from substrate limitation or from changes in population size, particularly the latter as temperature increases over the growing season.

Effects of soil moisture on soil respiration

This study shows that low soil water contents limit the response of SR to soil temperature. López *et al*. (1998), who studied the effect of drought on fine root dynamics in a Mediterranean forest in Spain, suggested that soil water availability is the main variable controlling root growth in these ecosystems, and not soil temperature as in many temperate forests. As has been observed in other studies on Mediterranean systems, root activity can be high during the autumn and even during the winter (López *et al*., 1998; Martínez *et al*., 1998). We also observed a maximum amount of live fine root mass in spring and autumn and a minimum amount in the summer (data not shown).

Soil moisture may limit SR in two ways, either by limiting aeration, and thus the diffusivity of air, when it is high or by stressing soil microbial communities and root respiration when it is low. At this site, soil moisture never seemed to reach a high limiting value but strongly limited SR during the summer months when the volumetric water content dropped below a value of 20% over 0–10 cm depth. A similar threshold value for soil moisture has been found in a ponderosa pine plantation in Northern California (Xu & Qi, 2001). This limitation by soil moisture to SR was clear, as SR peaked sharply immediately after rainfall events to its highest values during the year. Similar phenomena have been observed elsewhere; for example, Holt *et al*. (1990) observed a threefold increase in SR immediately after heavy rains. Law *et al*. (2001) found a similar phenomenon in a ponderosa pine forest during a summer drought, but the increase in SR had disappeared after 24 h of the rainfall event.

The stimulation may partly result from the displacement of air rich in CO_2 from within the soil and from the activity of microbes that oxidize the C dissolved in water, but the main effect is likely to result from stimulation of SOM decomposition after a period of drying, together with the rapid response of microbial biomass to increase in soil moisture (Birch, 1958, 1960; Anderson, 1973; Orchard & Cook, 1983). This phenomenon is often called the 'Birch effect', following the initial investigations by Birch. The most responsive component after summer rainfall events in our study was the SOM component. The reduction in SR as a result of drought may therefore vary largely from year to year depending on the number and intensity of rainfall events during the summer months. The frequency of random rainfall events during the summer months may be a critical factor determining total annual SR and therefore the whole carbon balance of the forest. Although this phenomenon may be of great importance in Mediterranean ecosystems, its consequences have not been quantified in terms of total annual NEE or its interannual variability, which is large in these Mediterranean ecosystems. The total annual amount of CO_2 respired by the soil during the year 2000 was *c.* 9 Mg C ha^{-1} which is within the range observed in other forests with similar mean annual precipitation and temperature (Valentini *et al*., 2000).

Modelling

SR has often been modelled using only soil temperature, and occasionally soil moisture, as the driving variables for particular sites (Epron *et al*., 1999b; Buchmann, 2000; Xu & Qi, 2001). In the field, soil temperature and soil moisture often co-vary. We observed that high temperatures occurred when soil moisture was lowest and that low temperatures generally coincided with high soil moisture contents. Despite this tendency, we found no clear relationship between soil moisture and soil temperature over the year, and SR was clearly related to either one or the other at any given time. During the winter, spring and autumn, soil temperature was a good predictor of SR, whilst during the summer months soil moisture was the best predictor of SR. This has also been observed in other studies in Mediterranean regions (e.g. Keith *et al*., 1997; Matteucci *et al*., 2000; Xu & Qi, 2001). Although several different functions have been proposed to describe the relationship between SR and soil moisture, depending on soil type and characteristics such as texture (Howard & Howard, 1993; Davidson *et al*., 2000), linear relationships have also previously been used successfully (Holt *et al*., 1990; Epron *et al*., 1999b). Whilst it is likely that temperature and moisture do co-vary during some periods of the year, particularly spring and autumn, we were successfully able to predict SR using a simple threshold switch between either the one or other of the two variables, and this explained more than 91% of the temporal variation in SR, indicating that these are the two dominant environmental variables influencing SR in this stand.

However, we were not separately able to predict with confidence root respiration and litter decomposition over the year in relation to changes in soil temperature and soil moisture, mainly for two reasons. Firstly, in this forest SR was dominated by the decomposition of SOM and belowground detritus. This is to be expected in a forest that has very recently been coppiced, with the result that NEE, and thus the carbon supply to the roots, has dramatically been reduced. Root respiration was consequently a small proportion of SR, making it more difficult to find clear relationships with environmental variables. Secondly, seasonal changes in the populations of active roots and microbes may have confounded the response to environmental soil variables (Trumbore *et al*., 1996). The annual course of root respiration may be only weakly related to that of soil temperature because the physiology and phenology of the trees may play more important roles in determining the amount of roots active at particular times of the year. For example, root respiration has been found to peak in late spring, coinciding not only with high temperatures but also with leaf flush, and to peak again in autumn prior to litterfall (e.g. Dickmann *et al*., 1996).

Soil moisture and soil temperature measured over 0–10 cm depth were good predictors of SR. It is likely that temperature and moisture over this interval are more closely coupled to changes in air temperature and precipitation than at greater depths. Soil profiles of root and microbial biomass at the site (data not shown here) demonstrated that most fine root and microbial biomass occurs within the top 10 cm of the soil, so that stronger relationships with temperature and moisture between 0 and 10 cm than at greater depths are to be expected. Although microbial and root respiration in deeper soil layers may also make an important contribution to the total SR, respiration at depth in the mineral soil is likely to be less dependent on changes in temperature or moisture content (Giardina & Ryan, 2000).

Contribution of the components to the total soil respiration

There is large variability in the literature with regard to the relative contributions of autotrophic and heterotrophic respiration to total soil CO_2 efflux (as reviewed by Hanson *et al*., 2000). Estimates of root respiration, for example, range from 22% (Tate *et al*., 1993) to as much as 90% (Thierron & Laudelout, 1996). As discussed earlier some of this large variability may be simply the result of differences in methodology, because it is difficult to measure the activity of roots without perturbing the soil, and partly the result of differences in forest and soil types (Hanson *et al*., 2000).

In this investigation, the main process contributing to SR was the decomposition of belowground litter and soil organic matter, which accounted for as much as 55% of the total SR. The contribution of aboveground litter decomposition ranged from 29% in the autumn, when rainfall was high and leaves started to fall, to 15% in the summer when low soil water contents limited litter decomposition. This seasonal variation in SR is in part related to the timing of leaf litterfall, as the input of fresh organic matter to the forest floor leads to the incorporation of soluble carbon and readily decomposable organic matter (Schlesinger, 1977).

The contribution of root respiration was minimum in spring and maximum in autumn, coinciding with rainfall events after the summer and periods of moderate temperature. The annual average contribution of 23% is rather low compared to previously reported figures. Ewel *et al*. (1987) and Epron *et al*. (1999a) found a 60% contribution of root respiration in a 29-year-old-slash pine plantation in Florida and in a 30-years-old beech forest in northern France, respectively. In a unique girdling experiment, Högberg *et al*. (2001) found that 54% of the carbon assimilated by Scots pine in the Swedish boreal zone was respired by roots. By comparing SR rates in a forest stand and in an adjacent stand where

the roots were killed with a herbicide, Nakane *et al*. (1996) estimated that root respiration contributed 50% of total SR. Together with other studies indicating similar figures, they suggested that the proportion of total SR respired by roots may be fairly constant in forests that are close to equilibrium.

We attribute the much smaller relative contribution of root respiration to total SR at the present site to the prior coppicing of the forest a year earlier. This was followed by a considerable decrease in NEE (measured with the eddy covariance technique by another team on the site) and in NPP, which was likely immediately to cause reduced availability of substrate for root respiration. On the other hand, the large inputs of litter and detritus, both above- and belowground, would be expected to lead to increases in the other components of soil respiration. Furthermore, the logging operation (decrease in LAI, and consequent increase in solar radiation) would have a large impact on the microclimate at the site, i.e. an immediate increase in soil temperature and decrease in soil moisture at the surface of the soil, which would have affected litter and SOM decomposition. Thus, the prior coppicing is likely to have stimulated SR at the time when root respiration would have been limited by substrate availability.

Increased death of roots as a consequence of the trenching treatment should have induced an increase in respiration by the decomposers of root debris that might have continued into the following year, and may have led to underestimation of the proportion of root respiration. To minimize this effect, we waited several months for the initial flush of CO_2 resulting from the treatment to dissipate but this may not have completely obviated the problem.

In order to get a rough estimate of this error, we have calculated the flux of CO_2 resulting from the decomposition of the fine roots killed as a result of the trenching. Based on a measure of the dry mass of fine roots (< 2 mm) of $0.36\,kg\,m^{-2}$ at the time of trenching, and the measured proportion of live fine roots of 38% at that time (data not published), we estimate the average dry mass of fine roots killed in the trenched plots to be $0.14\,kg\,m^{-2}$. Then, we assumed a decomposition constant of $0.4\,year^{-1}$, based on Silver & Miya (2001) and estimated the annual average rate of respiration from this amount of dead fine roots during the year 2000 to be $0.07\,\mu mol\,m^{-2}\,s^{-1}$. This is *c.* 3% of the average CO_2 efflux measured in the NR and NLNR plots so that we may have underestimated the fine root respiration component by no more than this amount. We did not have an estimate of the coarse root biomass at the site, so we are not able to estimate the error resulting from decomposition of the killed coarse roots, but it is not likely to be large because of its much longer turnover constant (Silver & Miya, 2001).

Another problem associated with removal of roots to enable estimation of their contribution to SR, is the elimination of root water uptake and hence a potential increase in soil water content compared to the control plots. However, we did not measure a significant or consistent increase in soil moisture in the trenched plots. This is somewhat surprising but may be because of generally low water extraction by roots in all plots after the logging. Furthermore, as a result of the logging, the forest floor was directly exposed to solar radiation, which would enhance evaporation from the surface of all the plots.

The results obtained in this experiment are consistent with other studies showing a close link between tree production and SR. Nakane *et al*. (1996) estimated the contribution of root respiration after clear-felling to be reduced by 30% and attributed this reduction, not to root death, but to reduced root activity as a result of a reduction in primary production. This hypothesis is also consistent with observations by Dickman *et al*. (1996) who found no reduction in fine root length and numbers when primary productivity was strongly reduced after coppicing poplar trees. Furthermore, the girdling experiment of Högberg *et al*. (2001) neatly showed that SR was strongly reduced within a few days of girdling the trees of Scots pine, thus demonstrating the dependence of root activity on the carbon supply to the roots.

In many ecosystem models, root respiration is simply estimated as a function of soil temperature. Whilst such a relationship clearly exists, carbon supply from leaves to roots as a result of ongoing photosynthesis drives belowground respiratory activity, which is then moderated by environmental variables within the soil. This study suggests that belowground activity is likely to be influenced by changes in soil temperature and soil moisture as a result of forest management activities. Such activities dramatically change aboveground productivity and, in turn, may influence the activity of roots and microorganisms in the soil.

Conclusions

Several conclusions can be drawn from this study:

1 In a coppice mixed oak forest, soil moisture is a critical factor controlling soil respiration. A simple empirical model including both soil temperature and soil moisture explained more than 91% of the observed annual variation in soil respiration. Soil respiration was solely controlled by soil temperature above a threshold value of 20% volumetric water content in the top 10 cm, and below that threshold by soil moisture.
2 Immediately after coppicing, the main contributor to soil respiration was the decomposition of belowground detritus and SOM which contributed about 55% of soil

respiration over the year. The small contribution of root respiration to the annual total SR (23%) was attributed to the reduction in NPP.

3 Root respiration was strongly affected by summer drought. Microbial communities within the soil seemed to be more responsive to sudden changes in soil moisture than root respiration and leaf litter decomposition.

4 Contrary to what has recently been found in other studies, we found that the sensitivity of root respiration to temperature had a Q_{10} value close to 2, somewhat lower than that of decomposition of belowground detritus and total soil respiration. Respiration is a relatively conservative process with a well-established Q_{10} in the region of 1.8–2.4, so that variation from this range is most likely to result either from substrate limitation or from changes in the population of respiring roots. Seasonal variation in root populations is different in Mediterranean ecosystems than in temperate climates, where precipitation is more evenly distributed through the growing season.

5 The highest soil respiration fluxes were generally observed in spring and autumn. During the summer months, all components of soil respiration were strongly limited by soil moisture. However, peak rates of soil respiration were measured in the summer immediately after rainfall events, suggesting that random rainfall events may play an important role in determining the annual net ecosystem exchange of carbon in Mediterranean forest.

6 Projected changes in precipitation pattern may have much larger effects on soil respiration and, in turn, on the carbon balance of Mediterranean forest ecosystems than projected increases in temperature. The results from this experiment indicate that possible future increases in temperature and decreases in precipitation may decrease annual soil respiration from these ecosystems.

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