Carbon dioxide fluxes across the Sierra de Guadarrama, Spain

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Abstract Understanding the spatial and temporal variation in soil respiration within small geographic areas is essential to accurately assess the carbon budget on a global scale. In this study, we investigated the factors controlling soil respiration in an altitudinal gradient in a southern Mediterranean mixed pine–oak forest ecosystem in the north face of the Sierra de Guadarrama in Spain. Soil respiration was measured in five *Pinus sylvestris* L. plots over a period of 1 year by means of a closed dynamic system (LI-COR 6400). Soil temperature and water content were measured at the same time as soil respiration. Other soil physico-chemical and microbiological properties were measured during the study. Measured soil respiration ranged from 6.8 to 1.4 μmol m^{-2} s^{-1}, showing the highest values at plots situated at higher elevation. Q_{10} values ranged between 1.30 and 2.04, while R_{10} values ranged between 2.0 and 3.6. The results indicate that the seasonal variation of soil respiration was mainly controlled by soil temperature and moisture. Among sites, soil carbon and nitrogen stocks regulate soil respiration in addition to soil temperature and moisture. Our results suggest that application of standard models to estimate soil respiration for small geographic areas may not be adequate unless other factors are considered in addition to soil temperature.

Introduction

The characterization of soil respiration (SR) response through time and space is increasingly important to identify dominant sources and sinks of carbon (C) and parameterize carbon cycling to represent forest–atmosphere interactions in global modelling studios (Cox et al. 2000; Goh 2004). In the last decade, major efforts have been made to understand the environmental drivers of soil respiration. Soil temperature (ST) and soil moisture (SM) explain most of the variation in this parameter (Davidson et al. 1998; Rey et al. 2002), but additional factors such as forest type, soil fertility, soil texture, stand age, plant photosynthetic activity and topography also affect soil respiration in forested ecosystems (Rodeghiero and Cescatti 2005; Dilustro et al. 2005; Tang et al. 2005a; Kang et al. 2003).

However, the identification of the environmental factors controlling the variability of SR still remains a difficult task surrounded by large uncertainties, especially for forest soil in mountainous regions and when it is necessary to consider the effects of disturbances associated with forest fires. This is of major relevance in the Mediterranean forest ecosystems that are highly vulnerable to climate change. Numerous studies along elevation gradients indicate that soil C concentrations or stocks increase with altitude in

mountainous terrains (Rodeghiero and Cescatti 2005; Garten and Hanson 2006). Field studies in the mountains of more arid areas indicate that soil moisture is an important factor controlling soil C stocks and fluxes in elevation gradients (Wang et al. 2000; Li et al. 2007). Topography-induced microclimates can affect SR rates by constraining microclimatic factors, such as soil temperature and moisture (Kang et al. 2003; Li et al. 2007). Other studies suggest that several chemical and biological factors such as nitrogen (N) and C dynamics co-varying with soil moisture regulate the spatial distribution of soil C losses through decomposition (Garten and Hanson 2006).

The purpose of this study was to investigate the main factors that control seasonal and spatial variation of soil respiration along an elevation gradient in the northern face of the Sierra de Guadarrama mountains (central Spain).

Materials and methods

Study site

The study took place in central Spain (Valsaín, Segovia), located in the northern face of the Sierra de Guadarrama (40°51'N, 4°3'W). The total area of the Valsaín forest is 10.672 ha, covered mainly by Scots pine (*Pinus sylvestris* L.). Other species present include oak (*Quercus pyrenaica* Willd.) and montane broom (*Cytisus purgans* (L.) Boiss.), with small areas of Holm oak (*Quercus ilex* subsp. *ballota* (Desf.) Samp.) and riparian forest. The herbaceous layer is largely made up of grasses, which develop in spring, dry off in summer and regrow to some extent after the first autumn rains.

The climate is nemoro-Mediterranean. The rainfall distribution is irregular, with a drought period in summer of approximately 2 months and an annual average rainfall of 1,600–1,400 mm. Mean temperatures range between 1.5 and 2.7°C during winter and 19.7 and 20.3°C during summer. Geologically, granites are predominant. Soils are classified as Humic Cambisols or Typic Haplumbrepts.

Experimental design

A transect was established in a 64 ha *P. sylvestris* L. watershed spread along an elevation gradient ranging from 1,320 to 1,592 m asl. Four sampling plots with dimensions 10 m × 15 m were designated within the experimental site. An additional site (plot 100) was selected at a higher elevation (1,700 m asl), an area that was burned 2 years previously (Table 1). The tree density was 220 tree/ha, with a mean height of 30 m and a mean diameter at breast height of 41 cm. The mean age of the stands was 120 years. The general aspect of the site was NE with a mean slope of 30%.

The leaf area index (LAI) was 6.42 $m^2 \ m^{-2}$. The historical meteorological data collected in the area found that temperature decreased by about 0.65°C for every 100 m and annual precipitation increased by about 100 mm for every 100 m (Lopez Arias M, personal communication). A summary of the site characteristics is given in Table 1.

Air temperature and precipitation during the experimental period were obtained from the weather station in Puerto de Navacerrada (1,860 m asl; Fig. 1).

Soil respiration, temperature and moisture measurements

Measurements of SR, ST and SM were conducted between spring 2005 and summer 2006 randomly in each forest plot on a monthly basis, using a closed dynamic system LI-6400 coupled to an LI-6400-9 soil chamber (LI-COR inc., Lincoln, NE, USA). Measurements were made between 10:00 a.m. and 16:00 p.m. to minimize the diurnal variation in soil respiration using PVC collars (10 cm diameter and 4.5 cm length), which were inserted into the soil at 2.5 cm depth (to avoid root severing), at least 1 week prior to investigation, and left in place throughout the course of the experiment. The measurement of SR consisted of placing the chamber on the collar, scrubbing the CO_2 to sub-ambient levels and measuring the flux rate as it rose from 15 ppm below to 15 ppm above the atmospheric value. Soil respiration sampling was not performed on days following a rain event to avoid an overestimation of the efflux due to CO_2 displacement from soil pores (Rey et al. 2002). A total of 12 collars were placed in plots 14, 22 and 42; whereas 9 collars were employed in plot 33 and 6 in plot 100.

Soil moisture content and soil temperature in the top 10 cm of soil were measured next to each soil respiration measurements with a time-domain reflectometry system (TRIMEGM, IMKO GmbH, Ettlingen, Germany) and a thermocouple sensor (Omega Engineering, Stamford, CT). Soil water content was measured at three points around each collar.

Soil properties

Soil sampling

In March 2006, soil samples were taken from three different sites in each plot. Five soil cores were extracted (10 cm deep × 8 cm diameter) beneath the organic layer and composited. Soils were kept separately in plastic bags and rapidly transported on ice in a dark cooler to the laboratory and stored in a refrigerator (4°C) prior to the sampling process.

Composite mineral samples were separated into two subsamples for the determination of physico-chemical and

Table 1 Summary of site characteristics of six study plots spread along an altitudinal gradient in a *Pinus sylvestris* L. forest in the northern Sierra de Guadarrama mountains

	Plot 14	Plot 22	Plot 33	Plot 42	Plot 100
Latitude (N, deg.)	40°50′58″	40°50′39″	40°50′59″	40°51′15″	40°49′15″
Longitude (W, deg.)	4°02′52″	4°02′52″	4°02′52″	4°02′34″	4°04′2″
Elevation (masl)	1,592	1,579	1,380	1,320	1,700
Slope (%)	22	50	20	67	49
Aspect (deg)	30°NNE	100°ESE	60°NE	110°ESE	–
Total porosity (%)	62	61	55	64	67
	b	b	c	ab	a
Particle density (g/cm^3)	2.57	2.64	2.63	2.64	2.54
	b	a	a	a	c
WFP (%)	58.4	50.5	51.9	45.0	28.8
	a	ab	ab	b	c
pH (1:2)	5.6	5.8	5.8	5.7	5.4
	b	a	a	ab	c
EC (µS/cm)	171	156	119	164	216
	ab	bc	c	bc	a
C STOCKS (kg C·m^{-2})	5.57 ± 0.16	7.76 ± 0.20	7.37 ± 0.30	5.34 ± 0.27	7.06 ± 0.30
	b	a	a	b	a
N STOCKS (kg N·m^{-2})	0.30 ± 0.01	0.34 ± 0.003	0.38 ± 0.01	0.27 ± 0.006	0.42 ± 0.02
	c	bc	ab	c	a
C/N	18.7 ± 0.4	23.1 ± 0.7	19.3 ± 1.4	19.4 ± 1.1	16.9 ± 0.2
	b	a	ab	ab	b
TOC (g/kg)	56.8 ± 1.6	75.3 ± 2.0	62.8 ± 2.6	56.8 ± 2.9	86.1 ± 3.6
	b	a	b	b	a
C-TMB (g/kg)	1.30 ± 0.23	1.14 ± 0.02	0.71 ± 0.05	0.60 ± 0.05	0.18 ± 0.008
	a	ab	bc	cd	d

Means with different letters within the site are significantly different, using Tukey's HSD at the 0.05 level

Fig. 1 Precipitation and mean temperature recorded during the experimental period. Data were obtained from the weather station in Puerto de Navacerrada located approximately 2 km from the site of the study
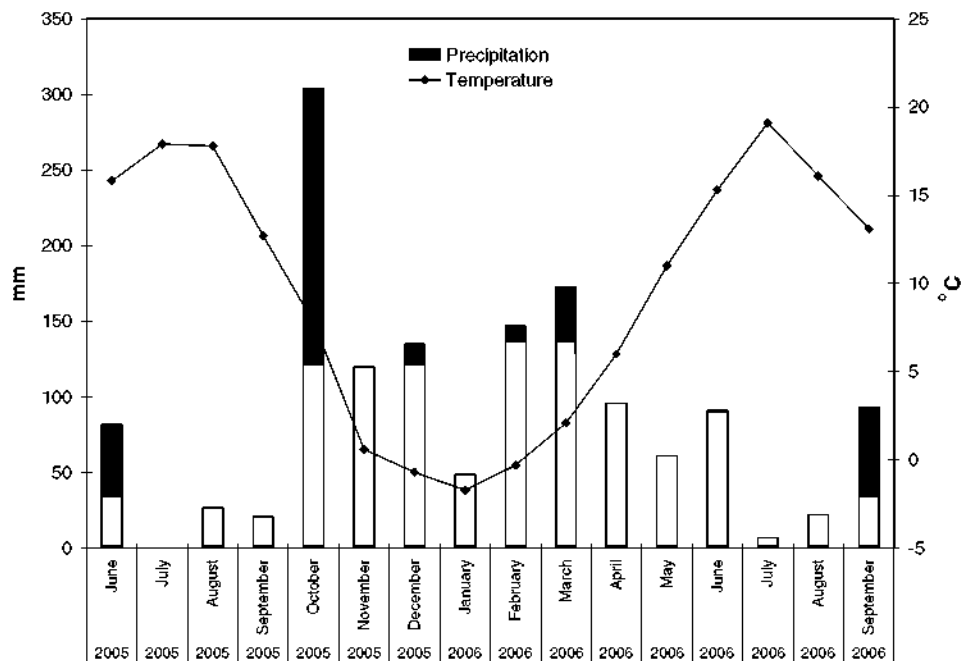
biological soil properties. The subsample for biological properties was sieved through a 2 mm mesh and stored at 4°C until they were processed. The remaining sample was air dried at room temperature for 2–3 days and sieved through a 2 mm sieve to remove stones, gravel and coarse debris. Soil passing the 2 mm sieve was grounded and homogenized using a mortar and stored in an airtight bottle prior to determining the physico-chemical properties.

Analysis of soils

Soil pH and electrical conductivity (EC) were measured in a 1:2 aqueous extract. The pH was measured by means of an ORION 720A pH-meter. Electrical conductivity measurements were performed by means of an ORION 115 conductimeter. The total C and N analyses were carried out by using a LECO TruSpec analyser. The organic carbon was analysed with a TOC-V_{CSH} analyser (SHIMADZU, Shimadzu Scientific Instruments, Kyoto, Japan).

Soil moisture content (SM) and dry density values were determined on separate and unaltered core samples taken at 50 mm depth using standard core steel samplers (28.5 mm internal diameter and 34.3 mm height). Soil bulk dry density was calculated from the dimensions of the samplers, taking into account the oven-dried weight as the known volume of soil. The soil moisture content or gravimetric water content was defined as the ratio of the weight of water and the weight of dry soil expressed as a percentage. The weight of water was determined as the difference between the weight of the sample and its weight after oven drying at 110°C for 24 h (UNE Standard 103-300-93). Water filling porosity (WFP) was calculated as: WFP = (w.c. × γ_s)/(1 − (ρ_d/γ_s)), where, w.c. is the gravimetric water content, γ_s is the soil particle density and ρ_d is the bulk dry density. The particle density or grain density was measured on a powdered oven-dried specimen using the pycnometer's method with water (UNE Standard 103-302).

Soil microbial biomass carbon was determined by microwave irradiation extraction method (Islam and Weil 1998). The organic carbon in the extracts of the control and microwaved soil were analysed with TOC-V_{CSH} analyser (SHIMADZU, Shimadzu Scientific Instruments, Kyoto, Japan). The total microbial biomass (C_{TMB}) was calculated as:

$$C_{TMB} = C_{EXTMW}/0.213$$

where C_{EXTMW} is the net flush of C, obtained from the difference between the extracted C in microwaved soil samples minus the extracted C in control soil samples, and 0.213 is a constant to compensate the fraction of extracted carbon by 0.5 M K_2SO_4.

Calculation of soil carbon and nitrogen stocks

Carbon and N pools (or stocks) in the top 10 cm of mineral soil (kg m^{-2}) were estimated by multiplying values of percent C and N in the mineral soil by soil-bulk density measurements from each plot.

Statistical analysis and modelling

Plot-level seasonal temperature response of SR was calculated by means of a Q_{10} function as mentioned by Janssens and Pilegaard (2003), which is called temperature sensitivity of SR:

$$SR = R_{10} \times Q_{10}^{((T-10)/10)}, \tag{1}$$

where SR ($\mu mol\ CO_2 \cdot m^{-2}\ s^{-1}$) is the soil respiration flux, R_{10} is the simulated SR at a soil temperature of 10°C, which is often used to compare the SR characteristics of ecosystems, Q_{10} is the temperature sensitivity of SR (the respiratory flux at one temperature over the flux at a temperature 10°C lower), and T is the measured soil temperature (°C). The functions were fitted to the measured data by means of a nonlinear least square fitter (Sigma Plot 6.0).

All statistical analyses were performed using the Statistica 6.0 software package (StatSoft. Inc., Tulsa. USA). Site (plot) and time effects for soil respiration, soil temperature and soil moisture were tested with a repeated measures analysis of variance (ANOVA). One-way analysis of variance was used to test for the effects of stand on soil respiration in the sites where there was no complete set of data available and to analyse the differences in soil properties between plots. The normal distribution and homogeneous variance were tested by the Kolmogorov–Smirnov and Levene's tests, respectively. Post hoc comparisons were tested using Tukey's HSD test, calculated at the 5% level. Whenever necessary, data were transformed as $(x + 1)^{0.5}$ or log x. Correlation analyses from the data of the entire data set were used to examine the relationship between soil respiration rates and soil properties.

Results

Soil respiration

Soil respiration values during the experimental period (June 2005–July 2006: Fig. 2) varied from 6.8 ± 0.2 $\mu mol\ m^{-2}\ s^{-1}$ in June 2005 to 1.4 ± 0.1 $\mu mol\ m^{-2}\ s^{-1}$ in February 2006. Soil respiration across the six study sites showed a typical seasonal pattern with maximums in spring and summer and minimums in winter. Seasonal patterns
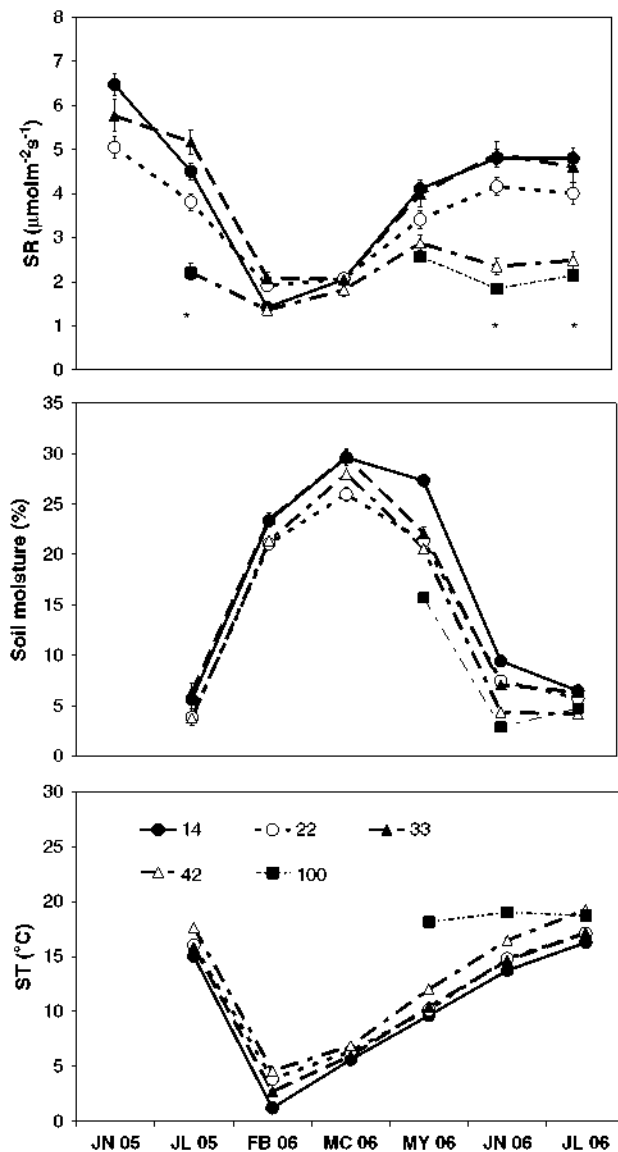
Fig. 2 Seasonal variations of observed soil respiration (SR, μmol m^{-2} s^{-1}), volumetric water content (SM, %), soil temperature at 10 cm soil depth (ST, °C) for study plots in Valsaín during the period 2005–2006. *Asterisk* indicates significant differences at the 0.05 level

were similar in the different plots, although temporal fluctuations were more limited in plots 42 and 100.

Repeated measures analysis of variance indicated that SR was different among sites ($F_{3,131}$ = 31, 871; P = 0.0) and time of the year ($F_{5,655}$ = 205, 29; P = 0.0). Mean values in plot 22 were intermediate (P < 0.05) between the highest values of plots 14 and 33 and the lowest values of plot 42 during July 2005, June 2006 and July 2006. Plot 100 showed low values (P < 0.05), similar to those found in plot 42, and significantly different from the rest of the plots.

Soil temperature and moisture

Both soil temperature and moisture content varied according to the season. Maximum soil temperature coincided with minimum soil moisture during the summer, and minimum soil temperatures were recorded in winter when soil moisture was highest (Fig. 2).

Soil temperature varied with site (P = 0.0), time (P = 0.0) and site over time (P = 0.0). There was a significant site effect (P < 0.05), with plot 42 exhibiting the highest soil temperature followed by plot 22, 33 and finally 14. Soil temperature was highest in July 2006, declined in June 2005, followed by May 2006 and March 2006, and dropped to a minimum in February 2006. Plot 100 showed the highest values during May 2006 and June 2006.

Soil moisture differed over time (P = 0.0), site (P = 0.0) and site over time (P = 0.0). Soil moisture was highest (P < 0.05) in plots 14 and 33 and lowest in plots 22 and 42. Soil moisture during May 2006 was higher (P < 0.05) in plot 14, while no significant difference was observed among the other plots. During June 2006, soil moisture was higher in plot 14 than in plot 42. For all treatments, soil moisture rose to a maximun in winter and spring months and declined steadily through June to a minimum in July.

Influence of temperature and moisture on soil respiration

Not surprisingly, both soil temperature and moisture were highly significant in a regression analysis explaining a large percentage of the seasonal variability in soil respiration. Soil moisture showed significant negative correlations to seasonal soil respiration for plot 14 (r^2 = 0.28, r = −0.53, P = 0.0), plot 22 (r^2 = 0.39, r = −0.63, P = 0.0), plot 33 (r^2 = 0.36, r = −0.60, P = 0.0) and plot 42 (r^2 = 0.06, r = −0.25, P = 0.0); while positive correlations were associated with plot 100 (r^2 = 0.10, r = 0.32, P = 0.0). Soil respiration was satisfactorily represented as a function of temperature, using the Q_{10}-type model fitted to the entire data set (Fig. 3). In plot 100, soil respiration and soil temperature were not correlated. The temperature-based Q_{10} models had similar Q_{10} values ranging between 1.30 and 2.04. The R_{10} values ranged between 2.0 and 3.61.

In plots 33 and 42, an interaction between soil temperature and soil moisture explained a 40 and 36% of the variability, respectively (Table 2).

Influence of soil parameters on soil respiration

Soil carbon stocks varied between 5.57 ± 0.2 kg m^{-2} (plot 14) and 7.76 ± 0.2 kg m^{-2} (plot 22), while soil nitrogen content varied from 0.27 ± 0.01 kg m^{-2} (plot 42) to 0.42 ± 0.02 kg m^{-2} (in plot 100; Table 1). Regarding

Fig. 3 Soil CO_2 efflux versus soil temperature as measured in Spanish Scots pine forest. The *solid line* represents the best fitting Q_{10} function. Functions were fitted through the entire data set. R^2 represents the proportion of variability in soil respiration explained by soil temperature
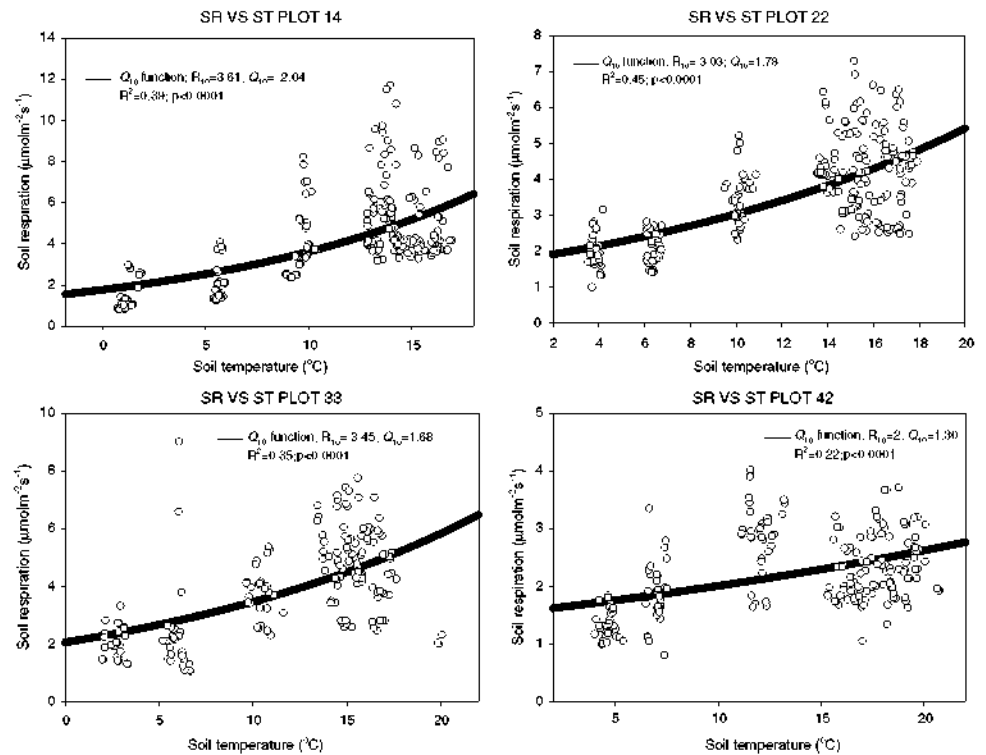

Table 2 Soil respiration as a function of temperature and moisture content, using a fitted linear curve through the entire data set

	Model	r^2	P
Plot 33	SR = 3.02 + 0.13 × ST − 0.04 × SM	0.40	0.0
Plot 42	SR = −0.19 + 0.13 × ST + 0.04 × SM	0.35	0.0

microbial biomass carbon (C-TMB), plot 14 showed the highest content, while the burned plot (plot 100) had the lowest. Soil respiration (Table 3) was positively correlated with C and N stocks and WFP, and negatively correlated to total porosity. Although not significantly, soil respiration tends to increase with C-TMB, TOC, pH and C/N.

Discussion and conclusions

The values of soil respiration in this area are in a range comparable with those measured in other Mediterranean forests (Rey et al. 2002; Rodeghiero and Cescatti 2005; Tedeschi et al. 2006). The annual Q_{10} derived from the data set were lower than the global median of 2.4 (Raich and Schlesinger 1992) and the range data (2.0–6.3) reported for forest ecosystems (Janssens et al. 2003). Our estimates of R_{10} (2.0–3.6) are in agreement with the range (0.7–4.9 μmol m^{-2} s^{-1}) observed in European forests (Janssens et al. 2003). We found similar Q_{10} and R_{10} values as were observed by Tang et al. 2005b and Rodeghiero and Cescatti 2005 in Mediterranean ecosystems. The reasons for

reduced temperature sensitivity in Valsain forest are unclear, and depend on the environmental constraints (generally low soil moisture content) and the substrate.

The results indicate that SR seasonal variation was mainly dominated by ST (Fig. 3) and that soil moisture also had an important influence on SR. However, the influence of SM on SR depends on the site. In plot 100, the temporal variation in SR was mainly controlled by soil moisture, and in plots 33 and 42 the interaction between ST and SM explained most of the variability observed. Although it is difficult to separate completely the influence of ST and SM imposed on SR, our short-term observation showed that SR responded mainly to ST in winter and that the interaction of soil temperature and moisture on SR was especially apparent during the summer months when low soil moisture limited soil microbial activity and root growth despite warm soil temperature (Fig. 2).

In the Valsain mountains, in situ measurements of soil respiration decline with declining altitude in contrast with other field studies that indicate correlations between SR and elevation (Wang et al. 2000; Rodeghiero and Cescatti 2005; Garten and Hanson 2006). Whereas the warmest temperatures were associated with the lowest elevation site (plot 42), the highest rates of SR were observed at the highest elevation plots (14, 22 and 33). The elevation factor alone may not explain the SR sensitivity by itself. Topography produces spatially heterogeneous SM and thus soil respiration. In our study, more mesic north-facing slopes (plot 14 and 33) showed higher SR relative to less

Table 3 Correlation coefficients between various soil variables and soil respiration (SR, μmol m^{-2} s^{-1}) at March 2006 in *Pinus sylvestris* L. forest in the Sierra de Guadarrama

	C.stocks (kg·C·m^{-2})	N.stocks (kg·N·m^{-2})	C/N	C-TMB (g·kg^{-1})	TOC (g·kg^{-1})	Particle density (g·cm^{-3})	Total porosity (%)	WFP (%)	pH (1:2)	EC (μS·cm^{-1})
SR	**0.65**	**0.65**	0.20	0.28	0.39	0.06	**−0.69**	**0.68**	0.48	−0.50
Q_{10}	0.32	0.35	0.06	**0.86**	0.26	**−0.64**	−0.18	**0.80**	−0.30	0.19
R_{10}	0.42	0.53	0.04	0.52	0.21	−0.53	−0.49	**0.72**	−0.14	−0.15

Bold numbers indicate a significant correlation at $P < 0.05$

mesic south-facing slopes (plot 22 and 42) despite higher ST at south-facing slopes.

The role of temperature and soil moisture in SR under field conditions is not always straightforward and my be influenced by vegetation covers, litter chemistry and thickness, soil organic matter, variable rates of below-ground root growth and activity, N availability and soil characteristics. All these factors potentially interact in complex ways through effects on decomposition. In our experiment, we obtained SR, Q_{10} and R_{10} values higher in the cooler, wetter site relative to the warmer, drier site. This is in agreement with Xu and Qi (2001). If we compare this trend with C-TMB (decrease in the same way), we could explain this behaviour by a faster response of the microbial community to warming when easily degradable substrate ability is also high.

In our experiment, the positive correlations between SR, Q_{10} and R_{10} values and C and N stocks, TOC, C-TMB and WFP (Table 3) indicated that microbial substrate quantity and nitrogen-rich conditions promote higher Q_{10} and SR values.

Atmospheric deposition and litter fall inputs could influence SR along the altitudinal transect.

Prior studies along the elevation gradient in Valsaín indicated a decline in litter fall inputs and N deposition with decreasing altitude (González Cascón et al. 1994; Garcia del Barrio et al. 1997). At low elevations, both higher mean annual temperatures and lower site N availability potentially contribute to lower soil C stocks and shorter turnover time for labile soil C. The highest values of SR in plot 14 also could be related to higher pine density and regeneration in this plot, and to differences in root respiration. Results from studies of other forests indicate that fine root biomass is directly associated with tree basal area (Chen et al. 2004).

Our results reveal that fire can alter the level of C, N, pH, and C-TMB in the soil. The increases in C concentration during the first years after the fire could be attributed to unburnt remains from dead roots, which slowly incorporate into the soil. C/N ratios were lower in the burnt soils than in the unburnt soils. Alteration of nitrogen by fire is a complex process. Fire alters the amount of nitrogen in the soil by volatilization of some into

the atmosphere and by converting the nitrogen into different nitrogen compounds. The pH decreased after the fire. The burnt plot exhibited reduced microbial biomass C compared to mature plots. This data revealed that fire altered the microbial diversity of the soil ecosystem. After the fire, C-TMB was very low, which indicates that microbial diversity had decreased significantly even 2 years after the occurrence of the disturbance. Decreases in microbial biomass have been widely reported after a fire. In the burnt plot, SR, Q_{10} and R_{10} were lower than in unburnt plots.

From the results obtained, it can be concluded that under similar climatic conditions and soil types within a small geographical area, variation in soil temperature, soil moisture, carbon and nitrogen stocks and C-TMB can influence SR in southern *Pinus sylvestris* L. forest. Thus changes in soil parameters over small scales need to be considered when modelling landscape-level SR. Furthermore, a better understanding of how natural disturbances affect C and N cycling is crucial for predicting how changes in climate and disturbance regimes will affect the exchange of C between forest ecosystems and the atmosphere.

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