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ECOSYSTEMS

Effect of Simulated Climate Change on Soil Respiration in a Mediterranean-Type Ecosystem: Rainfall and Habitat Type are More Important than Temperature or the Soil Carbon Pool

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ABSTRACT

Soil respiration (R_S) is known to be highly sensitive to different environmental factors, such as temperature, precipitation, and the soil carbon (C) pool. Thus, the scenario of global change expected for the coming decades might imply important consequences for R_S dynamics. In addition, all of these factors may have an interactive effect, and the consequences are often confounded. We performed a field experiment to analyze the effect of soil moisture and habitat type on R_S in a Mediterranean-type ecosystem by simulating three possible climate scenarios differing in the precipitation amount during summer (drier, wetter, and current precipitation pattern) in the main successional habitats in the area (forest, shrubland, and open habitat). We also considered other factors that would affect R_S, such as the soil C pool and microbial biomass. By the use of structural-equation modeling (SEM), we disentangled the interactive effects of the different factors affecting R_S. A higher simulated precipitation boosted R_S for the different habitats across the sampling period (14.6% higher respect to control), whereas the more severe simulated drought reduced it (19.2% lower respect to control), a trend that was similar at the daily scale. Temperature had, by contrast, scant effects on R_S. The SEM analysis revealed a positive effect of moisture and canopy cover on R_S, whereas the effect of temperature was weaker and negative. Soil C pool and microbial biomass did not affect R_S. We conclude that the precipitation changes expected for the coming decades would play a more important role in controlling R_S than would other factors. Thus, the projected changes in the precipitation pattern may have much more profound direct effects on R_S than will the projected temperature increases.

Key words: CO_2; climate change; drought; irrigation; microbial biomass; temperature; soil carbon; SOM.

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INTRODUCTION

Soil respiration (R_S) plays a critical role in regulating atmospheric CO_2 concentrations and climate dynamics at the global scale. After gross primary productivity, R_S is the second most important carbon (C) flux in ecosystems and is therefore an important component of the global C balance (Schimel 1995). R_S rates are known to be highly sensitive to different environmental factors, but especially to temperature and precipitation regime (Davidson and others 1998; Rey and others 2005; Inglima and others 2009; Phillips and others 2011). Thus, the warmer and drier future climate expected for the coming decades in some areas (IPCC 2007) might have important consequences for R_S dynamics (Rey and others 2005; Shen and others 2009). In general, it is expected that rising temperatures will increase R_S (de Dato and others 2010), although this effect is not clear enough (Giardina and Ryan 2000) and might be modulated by rainfall patterns (Talmon and others 2011; Thomey and others 2011). Nonetheless, despite the greater efforts in the last few decades to understand the processes that control R_S and its potential changes under a global-change scenario, there is still information needed for arid, semiarid, and Mediterranean ecosystems and, overall, for ecosystems where water availability and primary production are drought-limited for a considerable period of time (Rey and others 2002; Cable and others 2008; Almagro and others 2009). This is important because they occupy one-third of the land surface area of the planet (Emanuel and others 1985) and are among the ecosystems most vulnerable to climate change.

The expected decrease in precipitation in the Mediterranean region is likely to strongly affect the C cycling in these ecosystems, especially by the regulation of root and microbial activities (Rey and others 2005; Davidson and Janssens 2006; Matías and others 2011). However, climate change is also augmenting variability of precipitation in many areas (Rodrigo 2002), and it is likely that the greater aridity in some regions will not preclude the possibility of occasional rainy years (Beniston and others 2007). These sporadic rainy years may strongly determine C cycling (Rey and others 2002; Cable and others 2008; Marañón-Jiménez and others 2011) and should be taken into account to determine future R_S dynamics. Similarly, R_S may be simultaneously affected by other global-change drivers, generating non-additive responses (Xu and others 2004; Saito and others 2009). In Mediterranean ecosystems, where the human alterations over centuries have produced several phases of habitat degradation (Kosmas and others 2002), land-use change becomes a key factor that may alter R_S (Euskirchen and others 2003; Almagro and others 2009) and that might interact with climate alterations (Zheng and others 2005). Thus, studies considering explicitly different combinations of precipitation regimes and habitat-degradation types are needed to properly assess future trends in CO_2 fluxes.

Soil moisture and temperature have been traditionally considered to be the main factors affecting CO_2 effluxes from soil to atmosphere (Davidson and others 1998; Lloyd and Taylor 1994; Curiel-Yuste and others 2004; Xu and others 2004). Besides the global importance of temperature and precipitation, other factors that influence R_S include habitat characteristics, microbial biomass, or the substrate where the microbial reaction takes place (Gough and Seiler 2004; Davidson and Janssens 2006; Casals and others 2009; Marañón-Jiménez and others 2011). Overall, denser canopy cover implies higher R_S (Reichstein and others 2003; Hibbard and others 2005), as well as greater microbial biomass or a higher soil C pool (Luo and Zhou 2006). In addition, all these factors may have an interactive effect (Harper and others 2005; Shen and others 2009), and their consequences are often confounded (Phillips and others 2011). All of these factors should be explicitly taken into account to properly determine possible variations in R_S. Thus, experimental analyses addressing not only the combined effect of these different factors but also their direct and indirect effects are needed to disentangle the complex relations influencing R_S and the consequences of global-change scenarios.

The complex relationships among R_S and its controlling factors can be explored in an integrated way by the use of structural-equation modeling (SEM). SEM is a statistical method that helps provide insights into complex theoretical issues. These techniques are typically used to confirm or disprove a model hypothesized a priori, that is, to test the statistical adequacy of a proposed causal model (Browne 1982; Hayduck 1987; Shipley 2000; Iriondo and others 2003), providing an overview of the factors and relations directly and indirectly affecting R_S. However, despite the great utility of SEM to disentangle this complex process, only a few studies have used it to determine the importance of the different factors implied on R_S (Murphy and others 2008; Saito and others 2009).

The objective of this article is to analyze the impact of both biotic (plants and microbial biomass) and abiotic (precipitation, temperature, and soil C pool) factors on soil respiration under a climate-change scenario in a Mediterranean-type ecosystem. For this, we performed a field experiment simulating rainfall variability according to different possible climate scenarios for the coming decades: (1) current conditions (no manipulation of water availability), (2) more severe summer drought according to a widely accepted IPCC scenario for the area, and (3) heavier summer rainfall simulating occasional rainy years (following the maximum average records for the study area). In addition, we performed the study in the main successional habitats in the area that differ in canopy cover (forest, shrubland, and open habitat) and characterized other factors that would affect R_S, such as the soil C pool and microbial biomass. Our general hypothesis posited that the changes in the precipitation pattern expected in coming decades might imply stronger consequences for R_S than changes in temperature or soil C pool in ecosystems characterized by a dry season, like the Mediterranean, because water might be the most limiting factor. To test this, we first analyzed the effect of precipitation variability, temperature, and canopy cover independently, and then their combined effect, together with the soil C pool and microbial biomass by the use of SEM. Four specific questions were posed: (1) What is the effect of the different climate scenarios on seasonal and daily R_S variation? (2) If any, are these effects consistent among the different habitats of the ecosystem? (3) Is the R_S dependence on temperature similar across the different climate scenarios? and (4) what are the main factors controlling R_S and how do they interact? By answering these questions, we seek to disentangle the complex relationships among R_S and environmental factors, and to determine the future direction of CO_2 emissions under contrasting ecological scenarios.

MATERIALS AND METHODS

Study Area

The study was conducted in La Cortijuela area, within the Sierra Nevada National Park (37°05′N, 3°28′W, Granada, SE Spain), with an elevation of around 1,650 m a.s.l. This mountainous area has a continental-Mediterranean climate, with cold winters and hot, dry summers. Rainfall is 816 mm y^{-1} (mean 1990–2007), concentrated mostly during spring and autumn. Vegetation in the area is composed of patches under different management, with a predomination of pine plantations, shrublands, open areas, and patches of native forest (see Matías and others 2009 for more details). These habitat types are representative of most Mediterranean mountains.

Experimental Design

We used a fully factorial field experiment crossing two main factors: habitat (as a surrogate for canopy cover) and climate scenario, each at three levels. With respect to habitat, we selected three common habitats in a Mediterranean mountain environment, differing in canopy cover: (1) open habitats: areas of bare soil or covered with sparse herbaceous vegetation, representing the lowest canopy cover; (2) shrubland: composed of the dominant shrubs in the study area, mainly *Crataegus monogyna* and *Prunus ramburii*, representing the mid-canopy cover; and (3) forest: composed of a mixed forest of *Pinus sylvestris*, *P. nigra* and scattered *Quercus ilex*, representing the denser canopy cover. For the climate-scenario treatment, we selected three levels differing in water availability: (1) Dry summer: based on the SRES A-2 model by the Intergovernmental Panel on Climate Change (IPCC 2007), according to which a reduction in summer rainfall of 30% is predicted for Mediterranean areas, as well as a longer dry period, beginning at the end of spring. For this treatment, we built rain-exclusion shelters following the design of Yahdjian and Sala (2002). The rainout shelters were erected from April to September to simulate longer and drier growing seasons; (2) Wet summers: to simulate rainy events, we marked out 2 × 2 m^2 with a watering system composed of four sprinklers, one at each corner. We simulated summer storms from mid-June to the end of September, watering weekly with 12 l m^{-2} of water. If a natural storm occurred at any time, the weekly irrigation pulse was not added. The total quantity of watering used throughout the summer was 180 l, equivalent to the mean summer rainfall of the five wettest summers of the 1902–2006 series in the study area (Matías and others 2011). Rainy summers like the one simulated by this treatment occur sporadically in the area (Matías and others 2011); and (3) Control: natural rainy conditions during the course of the experiment were studied by marking out 2 × 2 m^2, which were exposed to current climate conditions with neither water addition nor exclusion throughout the experiment, and thus this scenario will hereafter be called *control*. In each of the three habitats, we marked out 18 plots, and assigned 6 of them randomly to each of the climate scenarios, thus, making a total of 54 plots (3 habitats × 3 climate scenarios × 6 replicates; see Matías and others 2011 for further details on experimental design). Precipitation during treatment applications (April–September 2007) was 365.5 l m^{-2} (above the mean value of the 1990–2008 series). Thus, precipitation in the dry summer scenario and wet summer scenario was 237.6 and 545.5 l m^{-2}, respectively (Figure 1, Online Appendix).

Summer Soil Respiration Across Climate Scenarios

In early May 2007, three PVC collars per plot (diameter 10.5 cm × height 9 cm; 162 collars in total) were inserted into the soil to approximately 5 cm depth. Soil respiration was measured seven times in 2007 (25 May, 22 June, 20 July, 15 August, 31 August, 26 September, and 26 October) during climate simulations. Measurements were made on the collars, taking the mean value of the three collars in the same plot, and were usually performed simultaneously from approximately 9 a.m. to 3 p.m., always 2 days after irrigation events. This time lag after irrigation allowed us to exclude the effect of pore degasification (Marañón-Jiménez and others 2011). We used two CO_2 analyzer systems: the manual EGM-4/SRC-1 (PP-Systems, Hitchin, UK) and an automated Li-Cor 8100 (Lincoln, NE, USA). The order of measurement and instrument was rotated among the three treatments over the campaigns. CO_2 measurements made with the PP-Systems were calibrated against the Li-Cor 8100. Data from the two different devices were well correlated ($R^2 = 0.86$), and those from the EGM-4 were corrected using the resulting linear regression (slope = 0.941).

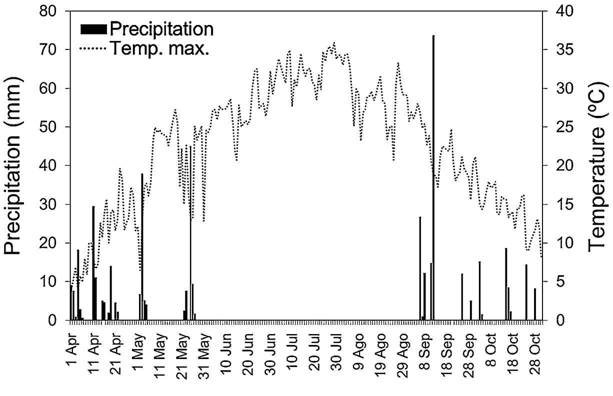

Figure 1. Daily rainfall and temperature in the study area during the sampling period. *Bars* represent rainfall and the *dotted line* represents the maximum daily temperature.

Soil Respiration over 24-h Cycles

Measurements of R_S over 24-h cycles allowed us to investigate the complete daily pattern of soil respiration in the different treatments and to find the dependence on temperature while other interacting environmental variables that can influence soil respiration (for example, phenological differences, soil moisture, microbial biomass and diversity, organic matter content) remained relatively constant. For this purpose, soil respiration was measured over a cycle of 24 h in one representative collar of each treatment, using the Li-8100 programmed to measure every 30 min. Soil temperature was measured every 30 min at 5 cm depth with a thermistor (TMC-HD, Onset Computer Corporation, Massachusetts, USA) connected to data loggers (HOBO H8, Onset Computer Corporation, Massachusetts, USA) within approximately 10 cm of the collar. Measurements were performed at the end of summer during nine consecutive days on the nine different treatments (14–23 September 2007).

Environmental Characterization

To characterize the environmental conditions associated with R_S measurements, the following parameters were measured in all study plots: soil temperature, soil moisture, canopy cover, microbial biomass, and the most important C fractions in soil: soil organic matter (SOM), total organic C (C_{org}), dissolved organic C (DOC). Soil temperature and moisture were recorded together with R_S at the different measurement campaigns (three measurements per collar). Temperature was measured with a digital thermometer probe at approximately 5 cm depth, and soil moisture by the time-domain reflectometry method (TDR-100, Spectrum Technologies Inc., Plainfield, Illinois) integrating from the surface to 20 cm deep.

Canopy cover was measured by hemispherical photography once during summer, when all leaves were completely expanded. Photographs were taken at ground level using a digital camera (CoolPix 5000, Nikon, Tokyo, Japan) aimed at the zenith with a fish-eye lens of 180° field of view (FCE8, Nikon). The images were analyzed using Hemiview 2.1 software (1999, delta-T Devices, Cambridge, UK) estimating the leaf area index (LAI), which gave us an estimate of canopy cover, ranging from 0 (bare ground) to 6 (dense forest).

To measure the soil C content and microbial biomass, soil samples were taken from the upper soil layer (0–8 cm) in May and August of 2007, coinciding with the periods of highest soil biological activity and severe drought, respectively. SOM was determined by incineration at 550°C with a thermobalance (Leco TGA 701) to constant weight (Sparks 1996), whereas total C was determined by combustion at 850°C (Leco TruSpec autoanalyzer), and total inorganic C was measured by acidification with $HClO_4$ in a TIC analyzer (UIC CM-5014). The difference between total C and inorganic C gave the C_{org}. DOC and microbial biomass (microbial C) were determined by the fumigation-extraction method (fumigation with $CHCl_3$ during 24 h and extraction with 0.5 M K_2SO_4; Jenkinson and Powlson 1976) and analyzed with a Shimadzu TOC-V CSH analyzer. Additional information on soil C analyses can be found in Matías and others (2011).

Data Analysis

The effect of the different climate scenarios on R_S and its variation across habitats was analyzed with a repeated-measure analysis of variance (rm-ANOVA) using habitat and climate scenario as between subject factors, and time (seven campaigns) as within subject factor. Wilk's Lambda was used for within subject interactions. Similarly, differences in soil respiration across climate scenarios and habitats were tested over 24-h cycles with a factorial ANOVA.

The effect of temperature on soil CO_2 fluxes was analyzed for all the continuous measurements performed over 24-h cycles on the different treatments. For this purpose, R_S from each campaign was fitted versus soil temperature (T_s) using the following equation describing the response of soil respiration to soil temperature (Curiel-Yuste and others 2004):

$$R_S = R_{15} Q_{10}^{T_S - 15/10} \qquad (1)$$

with two fitting parameters: R_{15} is the respiratory flux predicted at 15°C and Q_{10} is the factor of increasing respiration for a 10°C rise in soil temperature.

To test the relative importance of different environmental factors on R_S, we performed a structural-equation model (Shipley 2000). Our working model proposed that the R_S is controlled by these main factors: soil moisture, soil temperature, vegetation canopy (calculated as LAI, it represents the whole plant effect, including autotrophic root respiration), microbial biomass and carbon pool in soil (as a latent variable indicated by C_{org}, SOM, and DOC). Mean values and ranges of the different factors are shown in Table 1. We also included in our model the effect of vegetation canopy on soil moisture, temperature, and C pool and the correlation between soil temperature and moisture (Figure 2). As soil C samples were taken in May and August, we included the R_S campaigns of 25 May and 31 August in our model (*N* = 108). As we did not found any effect of soil C pool or microbial biomass on R_S (see results below), we ran the model again without these two factors, but including data from all the measurement campaigns (*N* = 378) to increase the model robustness. All variables were assessed for normality prior to statistical analyses, and suitable transformations (log, arcsin) were performed when necessary to improve normality according to Zar (1984). The maximum-likelihood method was used to estimate the standardized path coefficients in our model (Shipley 2000). The degree of fit between the covariance in the observed data with that expected if the working model is true was first examined by a goodness-of-fit χ^2. Non-significant χ^2 indicates that the pattern of covariance predicted by the hypothesis is no different from observed data, and thus the model could be accepted. In addition, the

Table 1. Summary Statistics of the Different Factors Used in the Path Analysis

	Units	Mean	Range
Canopy (LAI)	–	1.16 ± 0.06	0.33–3.05
Temperature	°C	14.29 ± 0.40	7.73–21.70
Moisture	%	17.31 ± 1.16	2.04–35.30
C_{org}	%	3.04 ± 0.06	0.81–4.34
SOM	%	6.69 ± 0.13	3.62–9.90
DOC	$\mu g\ g^{-1}$	34.37 ± 2.88	1.97–169.60
C_{micro}	$\mu g\ g^{-1}$	61.77 ± 2.26	12.28–130.73

Canopy (Leaf Area Index: ranging between 0 and 6, unitless); soil temperature; soil moisture (volumetric water content); C_{org} organic carbon; SOM soil organic matter; DOC dissolved organic carbon; C_{micro} microbial carbon pool in soil. Mean values are given ±SE, N = 108.

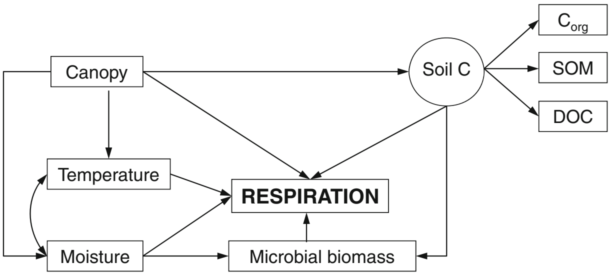

Figure 2. Path diagram representing the hypothesized causal relationships among environmental variables (*canopy* canopy cover; C_{org} organic carbon; *SOM* soil organic matter; *DOC* dissolved organic carbon; *microbial biomass* microbial carbon pool in soil) and soil respiration. C_{org}, SOM, and DOC were combined into the latent variable soil C (carbon pool in soil). The full model also includes the possible interactive or correlative effect between the different variables.

Bentler–Bonnet normed fit index (NFI) and the goodness-of-fit index (GFI) were used, as they are not affected by the number of subjects and the estimation method, respectively (Bentler and Bonnet 1980; Tanaka and Huba 1985). NFI and GFI range between 0 and 1, and values greater than 0.9 indicate a good fit of the model to the data. Path analysis was conducted using AMOS 5.0 (Arbuckle 1994) and all other analyses with JMP 7.0 software (SAS Institute). All analyses were run with mean values of the three collars per plot. Throughout this article, values of R_S are expressed in units of µmol m^{-2} s^{-1} and mean values are followed by ±SE.

RESULTS

Effect or Treatments on Environmental Variation

Pooling all scenarios, soil moisture significantly differed between habitats ($F = 26.20$; $P < 0.0001$), with higher values in forest (24.5% ± 0.4) than in shrubland (22.9% ± 0.3) or open (21.6% ± 0.3). Climate-scenario simulations implied different soil moisture in the experimental treatments ($F = 47.31$; $P < 0.0001$) from May to October (mean volumetric water content was 21.2% ± 0.3 in dry, 23.4% ± 0.4 in control and 25.0% ± 0.3 in wet, pooling all habitats). No interactions appeared between habitat and climate scenario ($F = 0.19$; $P = 0.95$), although differences across scenarios were higher during summer (Online Appendix). Soil temperature differed across habitats ($F = 15.9$; $P < 0.0001$), with higher values in open (15.4 ± 0.4) than in shrubland (13.4 ± 0.3) or forest (12.7 ± 0.3), but not across climate scenarios (F = 2.1; $P = 0.12$). Canopy cover (measured as LAI) differed across habitats ($F = 339.1$; $P < 0.0001$), with higher values in forest (1.91 ± 0.06) than in shrubland (1.18 ± 0.03) or open (0.41 ± 0.01), but not across climate scenarios ($F = 0.41$; $P = 0.66$).

Effect of Habitat Type, Water, and Temperature on R_S

R_S differed across habitats over the sampling period (Table 2), these values being higher in forest (4.96 ± 0.22) than in shrubland (3.96 ± 0.16) and open (3.71 ± 0.19). In the same way, these values differed between climate scenarios (Table 2), with the highest value for the wet scenario, followed by control and dry (5.09 ± 0.21, 4.44 ± 0.23, and 3.59 ± 0.19, respectively; Figure 3). Thus, the wet summer simulation augmented R_S by 14.6%, whereas severe drought reduced it by 19.2%. This pattern was consistent over the different habitats, as reflected by the lack of interaction between these two factors (Table 2). We also found a strong temporal variation in R_S over the sampling period, respiration being highest at the end of spring and decreasing during summer (Figure 3). In October, when climate-scenario simulations were not applied, R_S values remained similar in all cases ($F = 0.11$; $P = 0.90$).

Table 2. Results of rm-ANOVA Using Habitat and Climate Scenario as Between Subject Factors, and Time as Within Subject Factor to Test the Effects on Soil Respiration

Factor	*F*	*P*	df
Habitat (*H*)	38.53	<0.0001	2, 45
Scenario (*S*)	45.54	<0.0001	2, 45
Time (*T*)	313.76	<0.0001	6, 40
$H \times S$	0.79	0.54	4, 45
$H \times T$	10.71	<0.0001	12, 80
$S \times T$	3.80	<0.0001	12, 80
$H \times S \times T$	0.60	0.93	24, 140
All between	21.41	<0.0001	8, 45
Intercept	7053.64	<0.0001	1, 45

Wilks' Lambda was used for within subject interactions. F value of the F statistic (approximate value of F adjusted for interactions); P critical probability of the analysis; df degrees of freedom of the numerator and denominator, respectively.

Over 24-h cycles, the same pattern across climate scenarios ($F = 162.30$; $P < 0.0001$) and habitats ($F = 28.47$; $P < 0.0001$) was maintained, with the highest R_S values in the wet scenario and lowest in dry (Figure 4). R_{15} values followed the same pattern, being highest in the wet scenario and lowest in the dry. Overall, R_S increased during the daytime hours and decreased during the night, although this pattern was more evident in the open habitat than elsewhere (Figure 4). In addition to this pattern across habitats and climate scenarios, we found a weak effect of soil temperature on R_S, indicated by low Q_{10} values ranging from 1.04 to 1.42 (Table 3). Overall, the temperature effect on R_S was stronger in the open habitat and minimal in shrubland (Figure 4).

Combined Effects on R_S

The proposed structural-equation model provided an excellent fit with the observed data, as indicated by its non-significant f value ($\chi^2 = 12.88$; $P = 0.17$) and by the goodness-of-fit indices (NFI = 0.98; GFI = 0.97). Squared multiple correlation for the model was high ($R^2 = 0.84$), explaining most of the variation in R_S. Soil moisture was the factor with

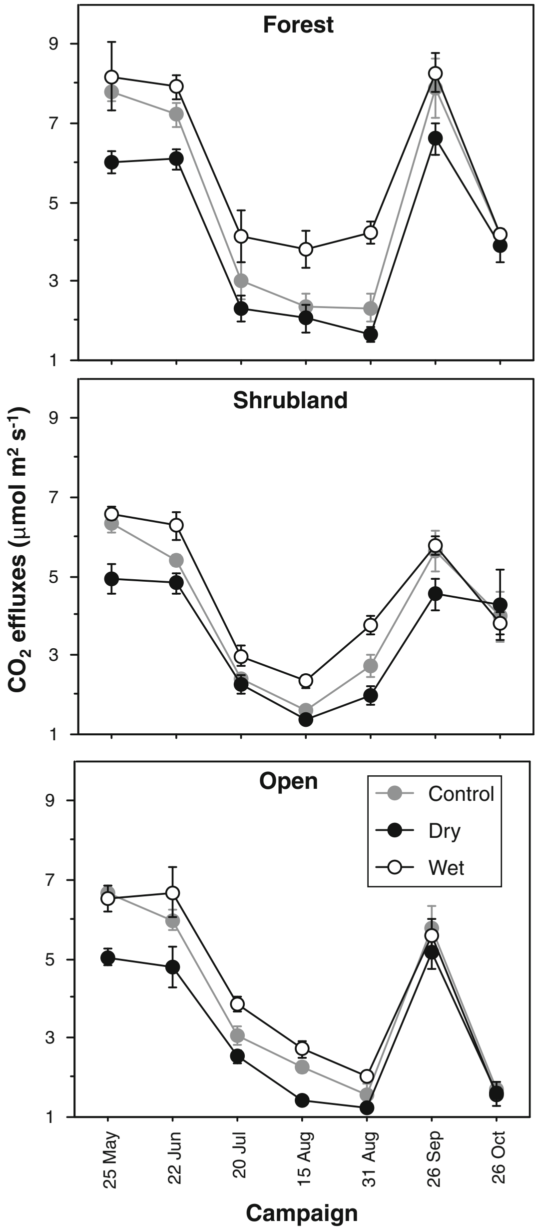

Figure 3. Temporal variation in soil CO_2 effluxes during the measurement campaigns for the different habitats among the different climate scenarios (*black dot* dry; *gray dot* control; *blank dot* wet). *Error bars* represents ±1 SE.

the strongest positive effect on R_S, whereas it was negatively affected by temperature, these two variables being negatively correlated (Figure 5A). Canopy cover, though showing a positive direct effect on R_S, also presented a positive effect on soil moisture and a negative effect on temperature and soil C pool. The soil C pool (indicated by C_{org}, SOM, and DOC) had no significant effect on R_S. Microbial biomass was determined mainly by the soil C pool, but did not have a significant effect on R_S. Besides these direct effects, the vegetation canopy indirectly affected R_S through temperature and moisture, having a stronger total effect than exerted in a direct way (direct effect = 0.27, indirect effect = 0.41, total effect = 0.68). When soil C pool and microbial biomass were extracted from the model and the complete data series was included, the same pattern was maintained (Figure 5B). Soil moisture remained as the most important factor, followed by vegetation canopy, whereas temperature had a negative effect.

Discussion

In this study, we have analyzed soil respiration across different climate scenarios varying in precipitation amounts that are possible for the coming decades, and across the most characteristic habitats in Mediterranean ecosystems. The range of R_S values obtained from the different habitats is similar to that measured in other ecosystems characterized by a strong dry season (Davidson and others 1998; Rey and others 2002; Marañón-Jiménez and others 2011). Soil CO_2 fluxes varied strongly during the period measured, with highest values in spring and basal values during summer. Overall, our results show that increased precipitation boosted R_S for the different habitats, whereas the simulated drier climate reduced R_S both at daily and seasonal time scales. In addition, by using SEM, we disentangled the interactive effects of the different factors affecting R_S and determined that soil moisture and habitat structure are the most important factors controlling it.

Precipitation Effect on R_S

In climate regimes characterized by cold, wet winters and hot, dry summers, water usually constrains biological activity in summer, and seasonal patterns of R_S are largely determined by soil water availability (Luo and Zhou 2006). This study shows that a decrease in soil moisture, both between the different campaigns at the seasonal scale and between the different climatic scenarios, significantly reduce the R_S. This pattern seems to be general in Mediterranean areas and other ecosystems with dry seasons (Rey and others 2002; Almagro and others 2009; Inglima and others 2009; Shen and others 2009; Marañón-Jiménez and others 2011). Variations in precipitation may alter root and microbial activities either by limiting aeration and air diffusivity when high or by stressing microbial communities and root respiration when low (Davidson and others 1998; Xu and Qi 2001; Rey and others 2002). In this study, we

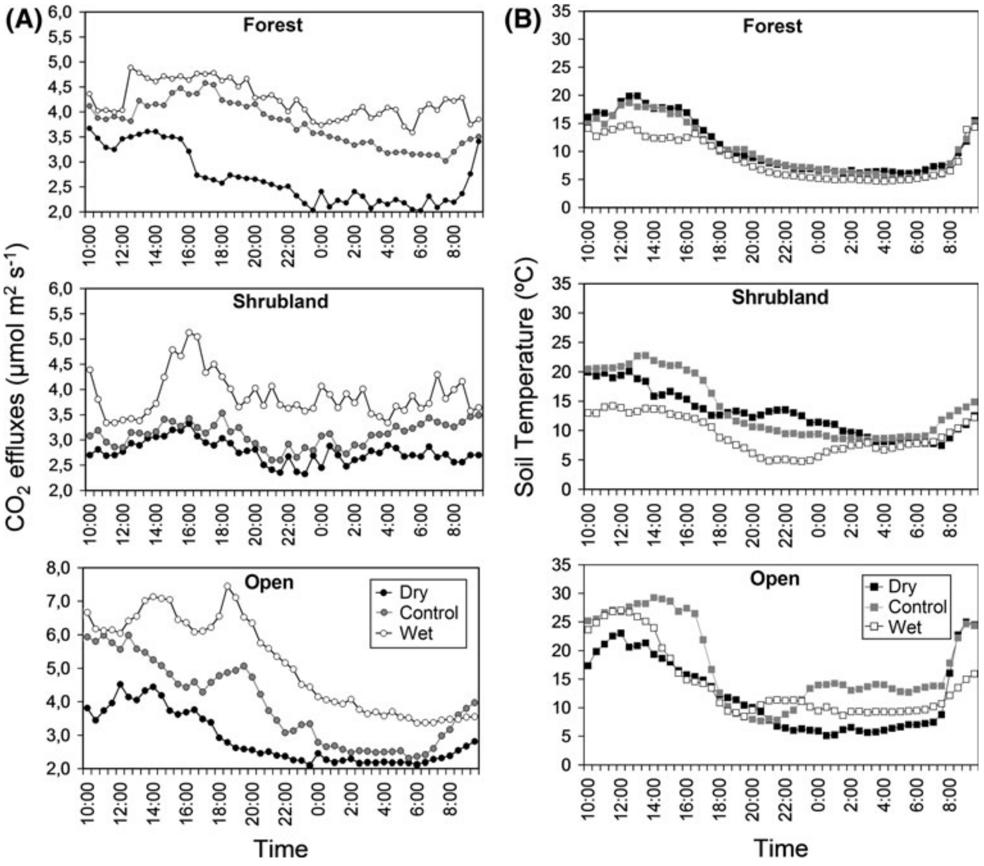

Figure 4. Half-hourly soil CO_2 effluxes (**A**) and soil temperature (**B**) during 24 h for the different habitats (*first panel* forest; *second panel* shrubland; *third panel* open) among the different climate scenarios (*black dot* dry; *gray dot* control; *blank dot* wet). Measurements started at 10:00 a.m. (local hour) and lasted 24 h during nine consecutive days on the nine different treatments (14–23 September 2007).

Table 3. Relationships Between Soil CO_2 Effluxes and Soil Temperature During a 24-h Cycle Among the Different Habitats and the Different Climate Scenarios Studied

Habitat	Scenario	R_{15}	Q_{10}	R^2
Forest	Dry	3.04 ± 0.03	1.42 ± 0.03	0.87
	Control	4.02 ± 0.07	1.17 ± 0.03	0.42
	Wet	4.57 ± 0.09	1.13 ± 0.03	0.28
Shrubland	Dry	2.81 ± 0.04	1.07 ± 0.03	0.10
	Control	3.10 ± 0.03	1.04 ± 0.01	0.17
	Wet	4.04 ± 0.13	1.07 ± 0.05	0.04
Open	Dry	3.07 ± 0.07	1.35 ± 0.05	0.60
	Control	3.56 ± 0.15	1.32 ± 0.06	0.42
	Wet	5.29 ± 0.18	1.26 ± 0.07	0.25

Measurements started at 10:00 a.m. (local hour) and lasted 24 h. Values of R_{15} and Q_{10} parameters were obtained by fitting measured CO_2 fluxes and simultaneous soil temperature to the exponential model of the equation (1) dependent on soil temperature. ±SE values for R_{15} and Q_{10} obtained from the model are indicated. R^2 is the coefficient of correlation between measured and modeled data.

found no evidence of limitation due to high soil moisture (soil VWC was 35.3% max) as increases in precipitation in all cases enhanced R_S both at the seasonal and daily scales (by 14.6 and 22.7%, respectively). On the contrary, a drier climate during summer and late spring as simulated in this study consistently decreased R_S by 19.2% at the seasonal scale and by 21.1% at the daily scale with respect to control, offering strong evidence of moisture limitation on this ecosystem and of the strong control of R_S by precipitation. In addition, other aspects of precipitation such as timing and intensity are expected to be altered in the future, with a potential increase of torrential events (IPCC 2007). This might also affect R_S (Sponseller 2007; Shen and others 2008; Almagro and others 2009), and could reduce R_S even more in the future.

Although this pattern remained consistent across the three studied habitats, there were pronounced differences among them. Forest was the habitat with the highest R_S and the strongest response to the wet scenario. The higher R_S may be explained by the lower radiation (lower soil water evaporation), the higher litter input (Matías and others 2011), the more vigorous root activity (Gough and Seiler 2004) and possible hydraulic lift in this habitat type (Querejeta and others 2007; Bauerle and others 2008). On the contrary, the open habitat is characterized by high radiation and hydric stress, diminishing respiration values with respect to the other habitats even under the wet scenario. Thus, these results highlight the necessity to explicitly take into

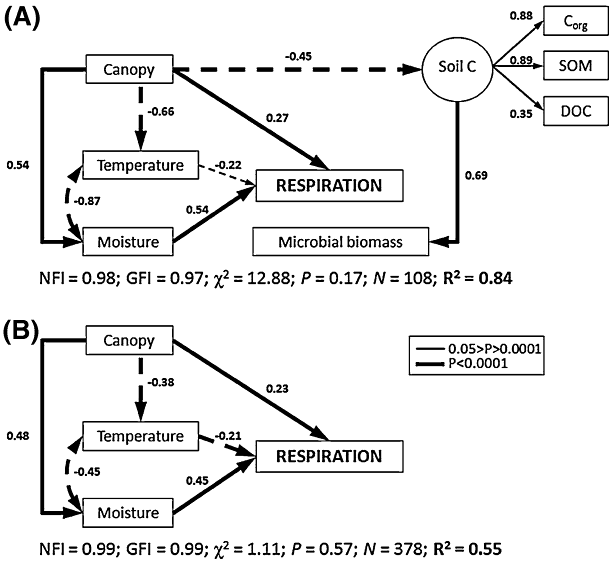

Figure 5. Path diagram representing the causal relationships obtained from the SEM model among environmental variables (*canopy* canopy cover; *soil C* carbon pool in soil; C_{org} organic carbon; *SOM* soil organic matter; *DOC* dissolved organic carbon; temperature; soil moisture; microbial biomass) and soil respiration. **A** Only the campaigns of 25 May and 31 August were included, whereas data from soil C pool and microbial biomass were not used in **B** and all campaigns were used. Positive effects are represented by *solid lines* and negatives are indicated by *dashed lines*, both with the standardized regression weights obtained from the SEM model indicated. *Arrow* widths are proportional to *P* values. Path coefficients non-significantly different from zero are omitted for simplicity. Fit statistics (*NFI* normal fit index; *GFI* goodness-of-fit index; *P* value; χ^2; R^2 squared multiple correlation) and sample size are given at the *bottom* of the path.

account the structural heterogeneity of the ecosystem to properly determine the response of soil respiration to environmental changes.

Temperature Effect on R_S

Temperature is a reliable indicator of R_S when no severe drought stress occurs (Moncrief and Fang 1999), but there is mounting evidence indicating a weak effect of temperature on Mediterranean ecosystems (Xu and Qi 2001; Rey and others 2002; Almagro and others 2009; de Dato and others 2010; Marañón-Jiménez and others 2011), as well as in other ecosystems characterized by a dry season (Talmon and others 2011). The low respiration responses to temperature variations found in this study (Q_{10} values ranging from 1.07 to 1.42) fit within the range of some studies in SE Spain (Almagro and others 2009; Marañón-Jiménez and others 2011), although lower than most studies in the Mediterranean (Raich and Schlesinger 1992; Reichstein and others 2002; Rey and others 2002). Overall, the highest Q_{10} values were found in the open habitat, where the daily temperature oscillation is higher than in the other habitats (as well as the daily R_S oscillation), being lower in forest and especially in shrubland. In addition to this low sensitivity to temperature, a negative relation was found between temperature and R_S (see comment below), indicating that higher temperatures do not imply increased respiration. Thus, in Mediterranean areas, a moderate increase of temperature as expected for the coming decades is unlikely to induce a greater R_S (de Dato and others 2010).

Combined Effects on R_S

The use of SEM enabled us to determine the combined effect of the different factors that may determine R_S and that are usually confounded (Harper and others 2005; Shen and others 2009; Phillips and others 2011). SEM analysis supports the result indicating precipitation as the most important factor determining R_S in Mediterranean ecosystems. Temperature and soil moisture showed a strong negative correlation, and for this reason we found a negative effect of temperature on R_S, as in other studies on arid and Mediterranean environments (Conant and others 1998; de Dato and others 2009; Saito and others 2009). In addition to soil moisture and temperature, vegetation canopy proved to be a strong factor determining R_S, not only by its direct effect (even stronger than temperature) but also by its indirect effect mediated by temperature and moisture (indirect effect = 0.41, total effect = 0.68). In Mediterranean-type and semiarid ecosystems, it is common for a high vegetation cover to increase soil moisture due to several processes such as evapotranspiration reduction, temperature decrease, or hydraulic lift (Bey 2003; Pyke and Andelman 2007; Querejeta and others 2007). In addition, the higher root activity may increase heterotrophic respiration (Hanson and others 2000; Högberg and others 2001; Gough and Seiler 2004). This result is consistent with the trend of increased respiration in those habitats with higher plant cover found in the Mediterranean (Almagro and others 2009; Inglima and others 2009).

The soil C pool and microbial biomass had, by contrast, no effect on soil respiration. This contrasts with results from temperate and cold environments, where R_S is influenced by the availability of C in the substrate (Conant and others 1998; Janssens and others 2001; Reichstein and others 2003; Campbell and others 2004; Murphy and others 2008). A weak relationship between R_S and soil C pool or microbial biomass was previously found by Casals and others (2009) in a Mediterranean ecosystem, although there are only a few studies exploring these relations in ecosystems characterized by a dry period, and the conclusions are not sufficiently clear (Balogh and others 2011; Talmon and others 2011). Probably, the differences with temperate ecosystems would be explained by the lower microbial biomass and soil C pool in Mediterranean areas, which might partially limit soil CO_2 fluxes, or by the small differences across habitats within this ecosystem type (Matías and others 2011).

Conclusions

Our results clearly showed that the precipitation changes expected for the coming decades would represent a more important role in the control of R_S than changes in temperature or soil C pool. Temperature may determine the final result of R_S only when soil moisture is not the limiting factor, which is not the common situation for most soils in Mediterranean-type and arid or semiarid ecosystems. Thus, projected changes in precipitation patterns may have much stronger effects on soil respiration in these ecosystems than the projected increases in temperature. In addition, besides the increasing efforts at estimating the soil C pool to determine future dynamics in R_S, our results indicate that its effect is very limited in Mediterranean environments, and that rainfall and canopy cover are the best indicators of R_S. This may be a common pattern for arid and semiarid ecosystems where the soil C pool is low and presents a pronounced dry period. This supports that models forecasting the effect of global change on soil CO_2 efflux on these ecosystems should focus more on changes in precipitation and habitat type than on the changes in soil C pool or in temperature.

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