

1. Introduction

Wildfires radically disturb carbon pools, leading to a sudden release of carbon to the atmosphere by combustion of vegetation and litter in soil (Brais et al., 2000; Conard et al., 2002; Page et al., 2002; Trabaud, 2004; Van der Werf et al., 2003).

Furthermore, after the fire the ecosystem acts as a source of carbon for months to years as soil respiration exceeds photosynthesis (Amiro et al., 2003; Bond-Lamberty et al., 2007; Harden et al., 2000; Litvak et al., 2003). The magnitude of the soil CO₂ efflux after the fire depends on climatic factors (Almagro et al., 2009; Davidson et al., 1998; Kirschbaum, 2000; Lloyd and Taylor, 1994) and the recovery of the vegetation (Irvine et al., 2007; Litton et al., 2003; Yanai et al., 2000). Overall, post-fire soil respiration increases with improving soil microclimatic conditions (non-limiting soil moisture and warm temperatures; Carlyle and Bathan, 1988), with the presence of carbon substrates in soil (Coleman et al., 2004; Franzluebbers et al., 2001), and with primary productivity of vegetation (Craine et al., 1998;

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Janssens et al., 2001; Knapp et al., 1998; Mkhabela et al., 2009).

Studies of the effects of fire on soil respiration are relatively abundant and often compare a burnt area versus a reference ecosystem (e.g. Dore et al., 2010; Hamman et al., 2008; Hubbard et al., 2004; Kobziar, 2007; McCarthy and Brown, 2006) or address the progression of soil CO₂ fluxes during ecosystem recovery (e.g. Gough et al., 2007; O'Neill et al., 2006; Yermakov and Rothstein, 2006). Despite the need to assess the impact of different forest management practises for sustainable carbon management (Peng et al., 2008), there is scant information about the effects of burnt wood management on soil respiration after wildfire (see Irvine et al., 2007; Mkhabela et al., 2009). Post-fire wood management has the potential to strongly affect the magnitude of the soil CO₂ efflux, as burnt logs, snags or coarse woody debris can determine key factors for respiration. For example, microclimatic conditions (soil moisture, soil temperature) can differ depending on the amount of woody debris scattered on the ground (Castro et al., 2011; Smail et al., 2008; Stoddard et al., 2008). Burnt wood also has a high nutrient content (Johnson et al., 2005; Kappes et al., 2007; Merino et al., 2003), which might improve soil fertility by providing nutrients and organic substrates (Coleman et al., 2004; Grove, 2003; Harmon et al., 1986), thus favouring microbial abundance and soil respiration rates (Hamman et al., 2008; Mabuhay et al., 2006; Trumbore et al., 1996). As a consequence of the above processes, vegetation cover and development may differ with burnt-wood management (Stark et al., 2006), which will also affect soil respiration (Burton et al., 2000; Nadelhoffer, 2000; Tang et al., 2005).

Salvage logging is a common post-fire silvicultural management practice for burnt wood around the world (Castro et al., 2011; Donato et al., 2006; Lindenmayer and Noss, 2006; Van Nieuwstadt et al., 2001). This practice consists of felling and removing burnt trunks, and is often combined with the elimination of the remaining woody debris (branches, logs, and snags) by chipping, grinding, mastication, or fire (Beschta et al., 2004; McIver and Starr, 2001). Salvage logging is employed for numerous reasons including silvicultural (e.g. site improvement for plantation or natural regeneration, access, fire risk prevention), economic (value of the salvaged wood products), aesthetics, and safety (Castro et al., 2010; McIver and Starr, 2001). Some of these justifications are controversial, however (Castro et al., 2010; DellaSala et al., 2006; Donato et al., 2006; Lindenmayer and Noss, 2006), and there is increasing support for less aggressive management policies for burnt wood in the post-fire landscape, based on the contention that burnt wood can enhance ecosystem functioning (Beschta et al., 2004; Castro et al., 2010, 2011; Donato et al., 2006; Lindenmayer and Noss, 2006). However, we are not aware of any study on the impact of salvage logging on soil CO₂ effluxes. This is a key question for optimizing post-fire forest restoration plans to mitigate the destruction of natural CO₂ sinks by wildfires.

In this study, we analyze the effects of different post-fire wood managements on the magnitude of soil respiration in a burned pine forest. We established three experimental treatments that differed in degree of burnt wood management, ranging from the conventional salvage logging to non intervention. We hypothesize that this will influence the magnitude of soil respiration, as the treatments contrast sharply in ecosystem characteristics such as microclimatic conditions and nutrient availability. Different elevations also imply a variation in the climatic conditions, which also may determine the vegetation composition, decomposition rates and nutrient dynamic in the ecosystem. For that, measurements were performed at seasonal intervals over the course of two years, and at two altitudes to assess spatial and temporal variation in soil respiration. Continuous 24-h campaigns and a watering experiment were also performed to discern the main factor (soil temperature versus soil moisture) determining differences in CO₂ effluxes among treatments. The

objectives of this study are: (1) to analyze the effect of post-fire burnt wood management on soil respiration at different altitudinal levels; (2) to determine the seasonal and daily patterns of soil CO₂ fluxes in this Mediterranean mountain ecosystem; and (3) to determine the roles of soil moisture and temperature on soil respiration across treatments.

2. Materials and methods

2.1. Study area

The study site is located in the Sierra Nevada Natural and National Parks (SE Spain), where the Lanjarón wildfire burned ca. 1300 ha of reforested pine between 35 and 45 years old in September 2005. Four sites of around 25 ha each along an altitudinal gradient were established to analyze the effect of burnt wood management on ecosystem regeneration and functioning (see Castro et al., 2010 for further details on experimental set-up). The lowest (LE hereafter) and highest (HE) elevations were selected for this study of soil respiration. LE is located at 1477 m a.s.l. (UTM position x, y: 456070; 4089811) and HE at 2317 m a.s.l. (UTM position x, y: 457719; 4091518). The pine species present before fire at each elevation differed, with *Pinus pinaster* and *P. nigra* dominating in LE and *P. sylvestris* in HE. The climate is Mediterranean-type, with rainfall concentrated in spring and autumn, alternating with hot dry summers. In LE, mean annual precipitation is 470 ± 50 mm, with summer precipitation (June, July and August pooled) of 17 ± 4 mm (1988–2008; climatic data from a meteorological station beside the site). Snow falls during winter, usually persisting from November to March above 2000 m a.s.l. The mean annual temperature is 12.3 ± 0.4 °C at 1652 m a.s.l. (State Meteorological Agency, period 1994–2008. Ministry of Environment) and 7.8 ± 0.7 °C at 2300 m a.s.l. (data from meteorological station placed in HE; period 2008–10). Both elevations were homogeneous in terms of fire intensity (high), aspect (southwest exposure), and bedrock (michaschists). The slope is between 25 and 30% in LE and 15 and 20% in HE. Tree density before burning was 1480 ± 50 ha⁻¹ for LE and 1060 ± 50 ha⁻¹ for HE, with a mean height of 6.36 ± 0.06 m and a mean d.b.h. of 13.34 ± 0.17 cm. No trees survived inside the study area, current vegetation is mainly composed of grass and forbs. The most common perennial species were *Ulex parviflorus*, *Festuca scariosa*, *Dactylis glomerata* and *Euphorbia flavicomica* in LE, and *Genista versicolor*, *Festuca* spp., and *Sesamoides prostrata* in HE.

2.2. Experimental design

From March to May 2006 (ca. seven months after the fire) we established in LE and HE three representative post-fire burnt wood management that differed in degree of intervention (treatments hereafter): (1) “salvage logging” (SL), trees were cut and the trunks cleaned of branches by chainsaw. Trunks were piled manually in groups of 10–12, and the woody debris was chipped by machine. Trunks were later removed from the site with a log forwarder, (2) “non-intervention” (NI), leaving all of the burnt trees standing. Trees fell naturally and progressively over the years, with $\geq 88.6 \pm 1.9\%$ still standing during this study; and (3) “cut plus lopping” (CL), a treatment where trees were felled (100% felled in HE; ca. 90% felled in LE), the main branches lopped off, and all wood left *in situ* on the ground. Burnt logs and branches diffusely covered around 45% of the surface at ground level (Castro et al., 2011). Each treatment was applied to a homogeneous area of at least 2 ha, adjacent to each other at each elevation.

In May 2007, 20 PVC collars per treatment at each elevation (diameter 10.5 cm × height 9 cm; 120 collars in total) were inserted

in the soil to ca. 5 cm depth, randomly distributed over an area of ca. 1 ha and separated by at least 10 m. For CL, we used a stratified random procedure, in which the collars were randomly installed in areas below the burnt branches. Soil respiration measurements were performed on the collars for purposes of determining two types of patterns: seasonal and diurnal.

2.3. Soil respiration across seasons

Soil respiration was measured in summer 2007 (four times), autumn 2007 (twice), spring 2008 (twice), summer 2008 (once), and autumn 2008 (once) in every elevation and treatment (see Appendix A for dates). During winter, snow prevented the access to the study area. Summer measurements were done under typical drought conditions, whereas spring and autumn represented the humid season for the area. Thus, calendar definitions of the seasons coincided with the influence of rainfall over the campaigns (see Appendix B for distribution of rainfall over the study period). Measurements were usually performed simultaneously in LE and HE (occasionally separated by one day), from ca. 9 am to 3 pm. We used two CO₂ analyzer systems: the manual EGM-4/SRC-1 (PP-Systems, Hitchin, UK); and an automated Li-Cor 8100 (Lincoln, NE, USA). CO₂ measurements made with the PP-Systems were calibrated against the Li-Cor 8100. A comparison was performed on 31 October 2007 in which simultaneous soil respiration records were taken alternatively with both instruments on the same collars ($n=48$, using collars of the three treatments). Data from the two different devices were correlated ($R^2=0.88$), and those from the EGM-4 (PP-Systems) were corrected using the resulting linear regression (offset = $0.197 \mu\text{mol m}^{-2} \text{s}^{-1}$; slope = 1.095). Soil CO₂ fluxes were taken together with soil temperature at ca. 5 cm depth (two measurements per collar; digital thermometer probe). The order of measurement was rotated among the three treatments over the campaigns. Vegetation inside the collars was not removed since it was considered an effect of the management treatment. Thus, soil respiration reported in this study could include some above-ground autotrophic respiration. Vegetation cover was estimated visually from 0 to 100% for each campaign (Sutherland, 1996). The effect of soil water content on soil respiration was explored using the rewetting index parameter (I_R) which has shown good correlation with CO₂ effluxes in a Mediterranean ecosystem (Almagro et al., 2009): $I_R = P/t$, where P is precipitation (mm) and t is time elapsed (days) between rainfall event and soil respiration measurements.

2.4. Diurnal patterns of soil respiration

Measurements of the diurnal CO₂ fluxes allowed us to investigate the complete daily pattern of soil respiration in the different treatments and to isolate the dependence on temperature from other interacting environmental variables that can influence soil respiration (e.g. herbaceous cover, phenological differences, soil moisture, microbial biomass and diversity, SOM content) remained relatively constant. For this purpose, soil respiration was measured over a cycle of 24 h in one representative collar of each treatment in HE, using the Li-Cor 8100 programmed to take a measurement every 30 min. Soil temperature was measured every 10 min at 5 cm depth with 4 thermistors (TMC-HD, Onset Computer Corporation, MA, USA) connected to data loggers (HOBO H8, Onset Computer Corporation, MA, USA) within ca. 10 cm of the collar. Temperature was averaged and synchronized every 30 min with the corresponding CO₂ flux value. Measurements were performed during the mid-summer (07/10–12/2007, representing dry conditions), late summer (09/16–19/2007, dry conditions before the end of the drought period, Appendix B) and late spring (06/27–29/2009, during the period of highest soil respiration according to the observed seasonal values from the previous year).

2.5. Experimental analysis on the effect of soil moisture

Given the evidence of strong effects of water availability and weak response to soil temperature derived from seasonal and diurnal campaigns (see Section 4), we performed a field experiment to disentangle the role of these two factors on soil CO₂ fluxes. In summer 2009, one week prior the experiment, four additional collars were installed randomly in each treatment in HE, separated by at least 10 m from each other and from the previous collars. At the beginning of the experiment, an area of 50 cm × 50 cm surrounding each of these collars was delimited and irrigated with 5 l of water, uniformly distributed over the 0.25 m² surface. The quantity of water (20 mm) was chosen to simulate a typical summer storm according to the record of storms registered for Sierra Nevada (Mendoza et al., 2009). Following water addition, soil CO₂ effluxes were measured on the irrigated collars to determine two types of patterns: across days and diurnal.

For patterns across days, we measured CO₂ fluxes (EGM-4), soil temperature (5 cm deep) and gravimetric soil moisture (10 cm deep) in three collars of each treatment one day before, just after, and 1, 3, 5, 7, 10, 15 and 20 days after irrigation (from 29-July to 19-August 2009), alternating the order of measurements in each treatment. Gravimetric soil moisture was calculated as the difference between wet and dry weight of the soil fraction < 2 mm after oven-drying at 60 °C to constant weight. For this, one soil sample at 0–10 cm depth was taken from within the delimited perimeter surrounding each collar on every sampling date. Simultaneously, CO₂ fluxes and soil temperatures were also measured in five non-irrigated collars in each treatment, which were taken as a drought-condition reference.

For diurnal patterns, we measured CO₂ fluxes (with the Li-8100) and temperature (with HOBO H8 loggers, 5 cm deep) at one collar of each treatment synchronized as described above. These measurements were carried out one day prior to irrigation, on the same day of the irrigation, and 3, 5 and 7 days after the irrigation. Three soil samples per collar (10 cm deep) were also taken on each of these days to determine gravimetric soil moisture.

3. Data analysis

3.1. Effects of treatments, seasons and altitudinal levels on soil respiration

The treatment effect on soil CO₂ effluxes and its variation across seasons was analyzed with a repeated-measure analysis of variance (rmANOVA) split-plot design, in which Treatment was considered the *main plot* factor, and Season (with five levels; summer 2007 and 2008, autumn 2007 and 2008, and spring 2008) the *subplot factor* (Potvin, 2001). The analysis was thus run with mean values per collar for each season. This allowed us to balance the design for the season factor and also produce integrated data of soil respiration per season. In any case, we also performed rmANOVA considering each date as a within factor level (10 campaigns), yielding similar results (data not shown; see Appendix A for values per date). Differences between elevations were tested for each season with one-way ANOVAs pooling data of the three treatments.

The relationship between soil CO₂ effluxes and herbaceous cover inside the collars was analyzed using a Spearman-rank correlation. The analyses were restricted to the two campaigns in the spring period (15-April and 19-May 2008: mean of $35.1 \pm 2.3\%$; all treatments, dates and elevations pooled), since herbaceous cover was very low in other seasons (summer: mean of $0.51 \pm 0.24\%$; autumn: mean of $9.0 \pm 0.8\%$; all treatments, dates and elevations pooled). Differences in herbaceous cover among treatments were tested with a one-way ANOVA for each date and elevation. The rela-

Table 1

Summary of repeated measures analysis of variance (rmANOVA) for the seasonal CO₂ fluxes. Analyses were performed with the mean value of CO₂ fluxes measured at each collar by season. df: degrees of freedom of the numerator and denominator, respectively. *F*: value of the *F* statistic. Approximate value of *F* adjusted for the Season * Treatment interaction (Wilk's-Lambda multivariate test). *P*: critical probability of the analysis.

Source	Low elevation			High elevation		
	df	<i>F</i>	<i>P</i>	df	<i>F</i>	<i>P</i>
Between-subject						
Treatment	2, 57	9.51	0.0003	2, 56	5.41	0.0071
Within-subject						
Season	4, 54	96.29	<0.0001	4, 53	227.65	<0.0001
Season * Treatment	8, 108	5.10	<0.0001	8, 106	9.77	<0.0001
Error	57			56		

relationship between the mean CO₂ flux for each date (all treatments pooled) and the rewetting index was tested using a Spearman-rank correlation.

3.2. Effect of experimental watering

The effect of experimental water addition on soil CO₂ effluxes and their variation across treatments and days after irrigation (time) was analyzed with a rmANOVA, with time defined as a within factor and treatment and irrigation as between factors (day before water addition were excluded of the analysis). Differences between treatments and time in soil moisture among the irrigated collars were similarly tested with rmANOVA. The relationship between soil moisture and CO₂ efflux in the irrigated collars was explored by Spearman-rank correlation. For this correlation, data measured in the first 2 h after irrigating were excluded from the analysis since we interpreted their rapid exponential decay as resulting from degassing of the CO₂ in soil pores displaced by water, an emission not directly associated with biological processes. This was evaluated by log-transforming the data of continuous CO₂ effluxes and fitting linear equations to the time course of these measurements (see Appendix C).

3.3. Effect of soil temperature

The effect of temperature on soil CO₂ fluxes was analyzed for all the continuous diurnal measurements, either in irrigated or non-irrigated collars. For this purpose, *F_c* 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 et al., 2004):

$$F_c = R_{15} Q_{10}^{T_s - 15/10} \quad (1)$$

with two fitting parameters: *R₁₅* is the respiratory flux predicted at 15 °C and *Q₁₀* is the factor of increasing respiration for a 10 °C rise in soil temperature.

Data were log or angular-transformed when required to improve normality and homoscedasticity (Quinn and Keough, 2009). Statistical analyses and models were made with JMP 7.0 software (SAS Institute). Throughout the paper, values of soil respiration are expressed in units of μmol m⁻² s⁻¹. Mean values are followed by ±1SE.

4. Results

4.1. Soil respiration across treatments, seasons and altitudinal levels

Soil respiration differed among treatments and seasons in both elevations (Table 1). At the lower elevation, respiration was

overall higher in CL (5.1 ± 0.4; all campaigns pooled) than in NI (3.52 ± 0.24) and SL (3.28 ± 0.22; Fig. 1). The same pattern was registered at the higher elevation, with higher values in CL (2.29 ± 0.16) than NI (2.07 ± 0.17) and SL (1.50 ± 0.10; Fig. 1). Among seasons, fluxes were much lower during summer than during spring and autumn for both elevations (mean of 2.08 ± 0.10 in summer, 6.8 ± 0.6 in spring and 4.45 ± 0.18 in autumn for LE; 0.79 ± 0.05 in summer, 2.35 ± 0.17 in spring and 2.91 ± 0.13 in autumn for HE; Fig. 1). An interaction emerged between treatment and season (Table 1), with CL clearly identified as the treatment with the highest soil CO₂ fluxes in spring (Fig. 1). Respiration was always higher in LE than in HE in all seasons (*P* ≤ 0.001, Fig. 1; mean of 3.97 ± 0.17 and 1.95 ± 0.09, respectively; treatments pooled).

Soil CO₂ fluxes were positively correlated with green herbaceous cover inside the collars for the spring campaigns (*ρ* = 0.41, *P* < 0.0001, *n* = 119 in LE and *ρ* = 0.28, *P* < 0.0028, *n* = 109 in HE). Herbaceous cover inside the collars differed among treatments. On 15 April, it was higher in CL than SL and NI for both elevations (76 ± 8%, 46 ± 8% and 35 ± 5%, respectively for LE; 47 ± 9%, 12 ± 2% and 11 ± 4% for HE; *P* ≤ 0.0004). On 19 May, the herbaceous cover in HE was also higher in CL than in NI and SL (24 ± 5%, 8 ± 2% and 4 ± 1%, respectively; *P* = 0.0002), whereas there were no differences among treatments in LE (56 ± 8%, 38 ± 5% and 50 ± 8%, respectively; *P* = 0.1828). For both elevations, soil fluxes were positively correlated with the rewetting index (*ρ* = 0.83 in LE and *ρ* = 0.98 in HE, *P* < 0.0001).

4.2. Effect of experimental watering

Soil moisture differed between sampling dates (*P* < 0.0001) and was similar among treatments (*P* > 0.05, no significant interactions). It peaked on the day of irrigation, and then decreased gradually in all cases (Fig. 2A). Irrigation stimulated soil CO₂ effluxes in the three treatments, with a strong effect of date (Table 2). For the irrigated collars, soil CO₂ effluxes spiked within 60 s after water addition, reached a peak on the same day (ca. 47 times the previous value before water addition) and fell rapidly during ca. 2 h due to soil pore degasification, which accounted for ca. 51–87% of emissions, depending on treatment, during the first 24 h after water addition (Fig. 3; see Appendix C). Respiratory fluxes then decreased towards basal values prior to the irrigation (Fig. 2B). Soil efflux peaks following irrigation were highest in CL, followed by SL, and were lowest in NI (Fig. 2B). Soil CO₂ effluxes in the reference collars without irrigation also varied with date (Table 2) but these effects can be attributed to a precipitation event that occurred thirteen days after the beginning of the experiment (12 August), which stimulated CO₂ effluxes and soil moisture measured on days 15 and 20 (14 and 19 August) of the experiment (Fig. 2C). Soil CO₂ effluxes in the irrigated collars were positively correlated to gravimetric soil moisture (*ρ* = 0.62, *P* < 0.0001).

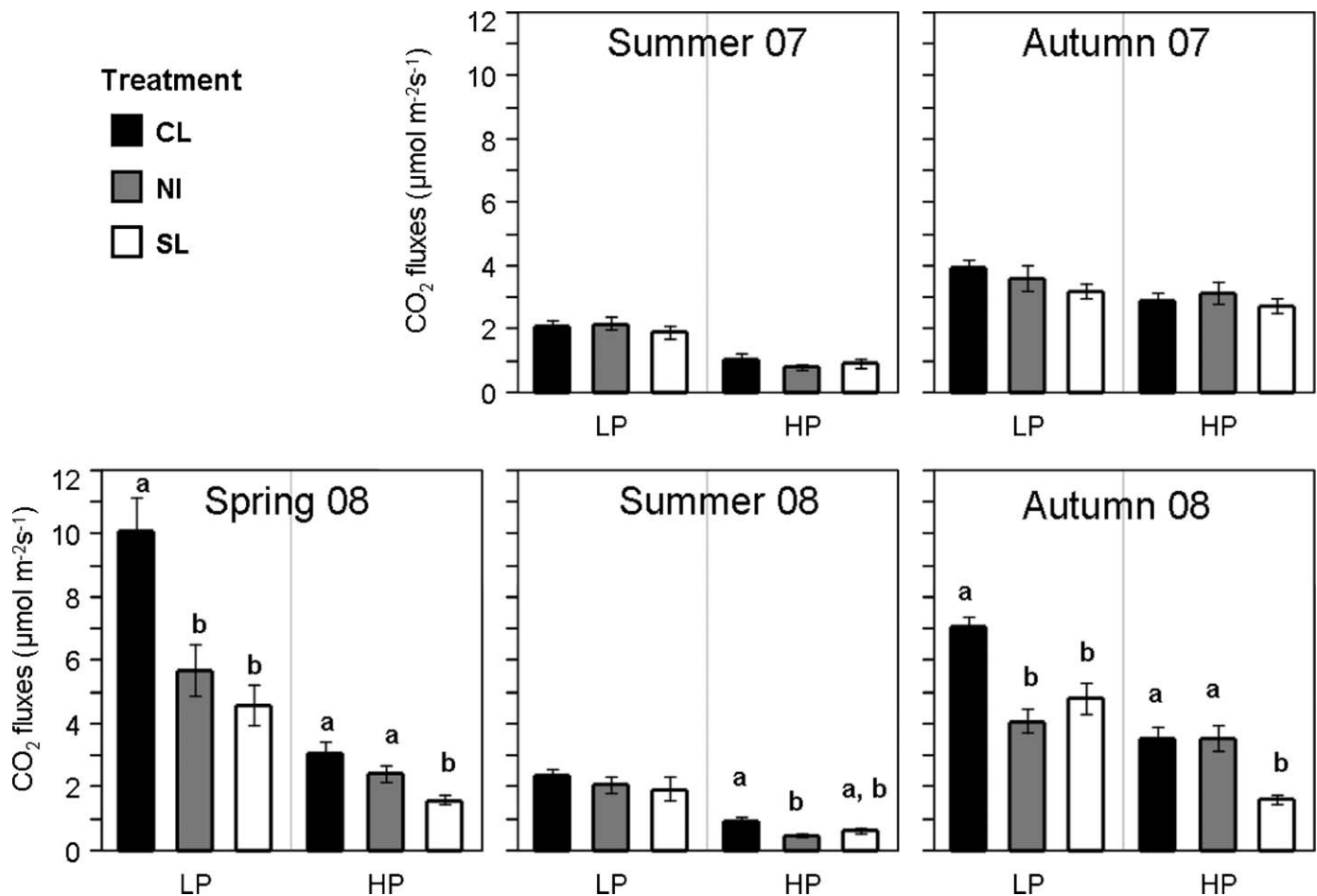


Fig. 1. Mean soil CO₂ effluxes in the different altitudinal levels and post-fire silvicultural treatments over the seasons. Abbreviations for altitudinal levels and treatments: LE: low elevation (1477 m a.s.l.); HE: high elevation (2317 m a.s.l.); SL: salvage logging; NI: no intervention; CL: cut plus lopping. Each bar represents the mean CO₂ efflux for the 20 collars per treatment and elevation. Standard error of each mean is represented over each bar. Different letters above bars indicate significant differences between treatments within elevation and season according to Tukey test after one way-ANOVA.

Table 2

Summary of repeated measures analysis of variance (rmANOVA) for CO₂ fluxes after experimental irrigation. df: degrees of freedom of the numerator and denominator, respectively. *F*: value of the *F* statistic. Approximate value of *F* adjusted for the Time * Treatment and Time * Treatment * Elevation interactions (Wilk's-Lambda multivariate test). *P*: critical probability of the analysis.

Source	df	<i>F</i>	<i>P</i>
Between-subject			
Irrigation	1, 16	13.93	0.0018
Treatment	2, 16	5.83	0.0125
Irrigation*Treatment	2, 16	6.94	0.0068
Within-subject			
Time	7, 10	32.04	<0.0001
Time * Irrigation	7, 10	41.68	<0.0001
Time * Treatment	14, 20	3.79	0.0023
Time * Irrigation * Treatment	14, 20	3.76	0.1037
Error	16		

4.3. Soil respiration sensitivity to diurnal temperature oscillations

Fitted values for the parameter Q_{10} were very low for all treatments and seasons (between 1.29 and 0.98, $R^2 < 0.10$ and $P > 0.05$ for most cases). Due to this lack of temperature dependence (Fig. 4), the parameter R_{15} showed the same pattern as the mean values of CO₂ fluxes, with the highest values registered in CL for all campaigns. Soil CO₂ fluxes under experimental watering also showed low tem-

perature sensitivity (Fig. 5). Overall, the temperature dependence of CO₂ fluxes increased very slightly in the absence of water limitations (3 days after irrigation) and fell again as the soil dried out (7 days after irrigation, Table 3). Again, R_{15} showed the same pattern as mean of the fluxes for every date, being always higher in CL, followed by NI and then SL (Table 3).

5. Discussion

In this study we have analyzed post-fire soil respiration considering burnt wood management and other environmental factors with the potential to affect respiration. The pattern of soil respiration was variable in time and space. On one hand, differences in altitudinal level yielded *ca.* twofold differences in respiration. On the other hand, soil CO₂ fluxes exhibited strong seasonality, with highest values in spring and basal values during the summer drought (see Almagro et al., 2009; Rey et al., 2002; for similar patterns). Overall, this study shows three main noteworthy factors that determine rates of CO₂ effluxes after fire in this Mediterranean ecosystem: (1) soil respiration is mostly determined by water availability, whereas soil temperature has a marginal effect; (2) soil respiration is substantially and consistently affected by burnt wood management; and (3) rain events during the dry season strongly impact soil CO₂ effluxes and reinforce the role of burnt wood management.

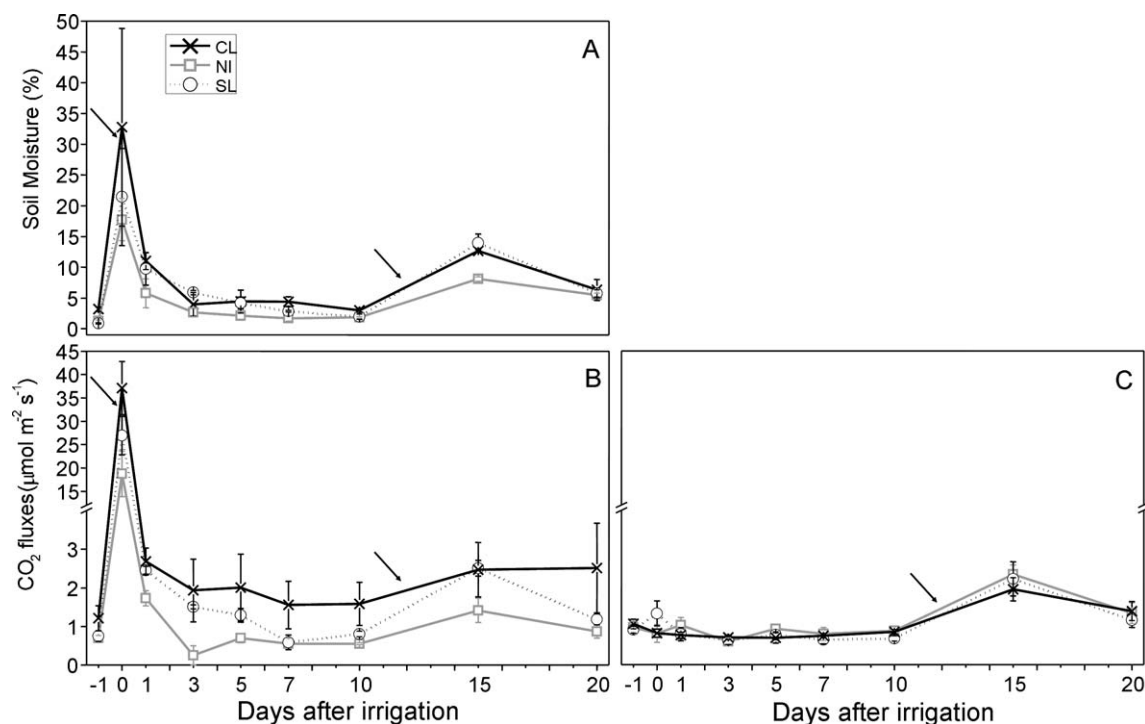


Fig. 2. (A) Soil moisture, (B) CO₂ effluxes in irrigated collars, and (C) CO₂ effluxes in reference collars not stimulated by water addition in the different post-fire silvicultural treatments several days after the experimental watering. Arrows indicate the days when the water addition was performed and when the natural rain event occurred. CL: cut plus logging; NI: no intervention; SL: salvage logging.

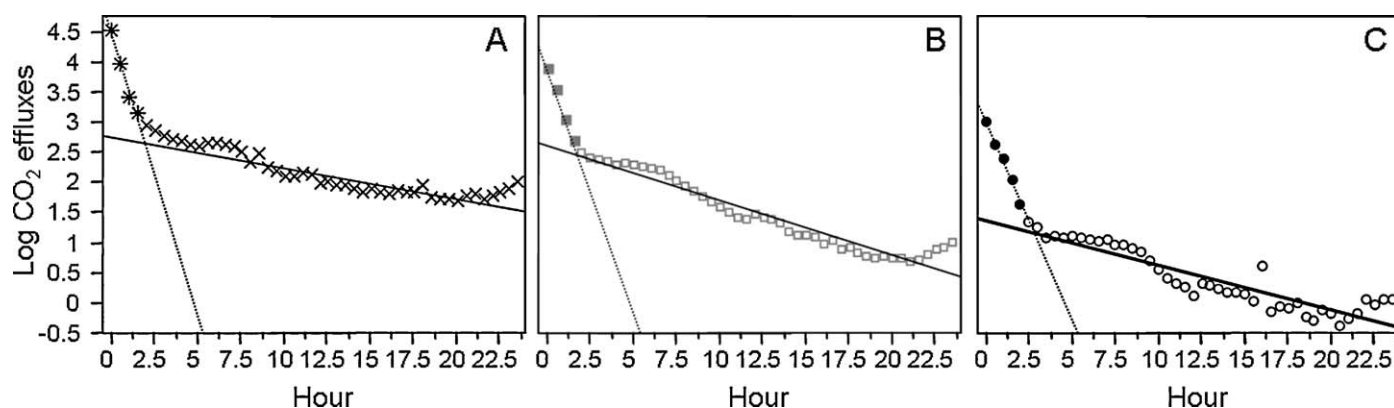


Fig. 3. Soil CO₂ effluxes (logarithmic scale) just after the water irrigation (9:00 am, local hour) over the first 24 h in (A) cut plus logging (CL), (B) no intervention (NI) and (C) salvage logging (SL). Open symbols and continuous lines correspond to effluxes and linear regressions during the respiration period (r) respectively, solid and asterisks symbols and dotted lines correspond to the linear regressions during the degassing period (d), respectively (see Appendix C). (Linear fitted equations for the respiration period: $Y = 2.752 - 0.0512 * X$, $R^2 = 0.81$ in CL; $Y = 2.591 - 0.0904 * X$, $R^2 = 0.93$ in NI; $Y = 1.352 - 0.0736 * X$, $R^2 = 0.82$ in SL; and for the degassing period: $Y = 4.456 - 0.9341 * X$, $R^2 = 0.97$ in CL; $Y = 3.851 - 0.8021 * X$, $R^2 = 0.99$ in NI; $Y = 3 - 0.6621 * X$, $R^2 = 0.99$ in SL.)

Table 3

Temperature sensitivity of daily soil CO₂ fluxes several days after the water addition treatment. Values of Q_{10} and R_{15} parameters were obtained by fitting measured CO₂ fluxes and simultaneous soil temperature to the exponential model of the Eq. (1) dependent of soil temperature. R^2 is the coefficient of correlation between measured and modelled data. Parameters for soil CO₂ fluxes during the day of water addition were not calculated, now that these fluxes are not temperature dependent but soil moisture dependent.

Treatment	Days after water addition	Soil moisture ^a (%)	Q_{10}	R_{15}	R^2
CL	1 day before	3.20 ± 0.35	1.00 ± 0.01	1.07 ± 0.02	0.01
NI	(summer drought)	1.24 ± 0.20	1.02 ± 0.01	0.95 ± 0.02	0.15
SL		0.86 ± 0.08	1.75 ± 0.19	0.02 ± 0.01	0.55
CL	3 days after	9.29 ± 1.54	1.07 ± 0.02	1.99 ± 0.08	0.25
NI		6.12 ± 0.08	1.07 ± 0.01	1.75 ± 0.07	0.37
SL		5.71 ± 0.82	1.10 ± 0.05	0.48 ± 0.06	0.29
CL	7 days after	4.02 ± 0.81	1.03 ± 0.01	1.23 ± 0.02	0.15
NI		2.91 ± 0.17	1.03 ± 0.01	1.22 ± 0.02	0.21
SL		1.94 ± 0.09	1.16 ± 0.04	0.17 ± 0.01	0.35

^a Mean of the gravimetric soil moisture of three soil samples taken inside the delimited perimeter of one collar per treatment.

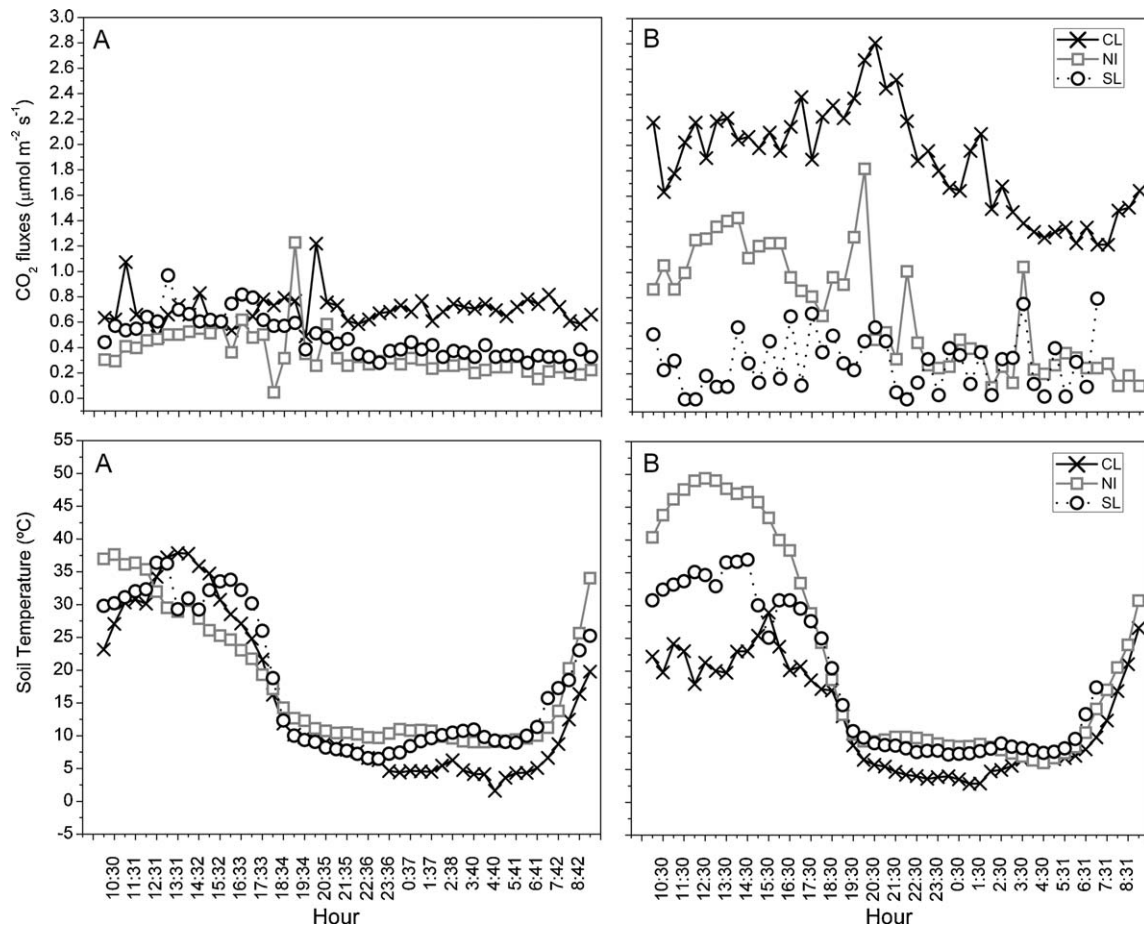


Fig. 4. Half-hourly soil CO₂ effluxes and soil temperatures in the highest elevation over 24 h. Two sampling dates are represented: (A) late summer (16–19 September 07); (B) late spring (27–29 May 09). Measurements started at 11:00 am (local hour) and lasted 24 h. (GMT is displayed in the x axes.) CL: cut plus logging; NI: no intervention; SL: salvage logging.

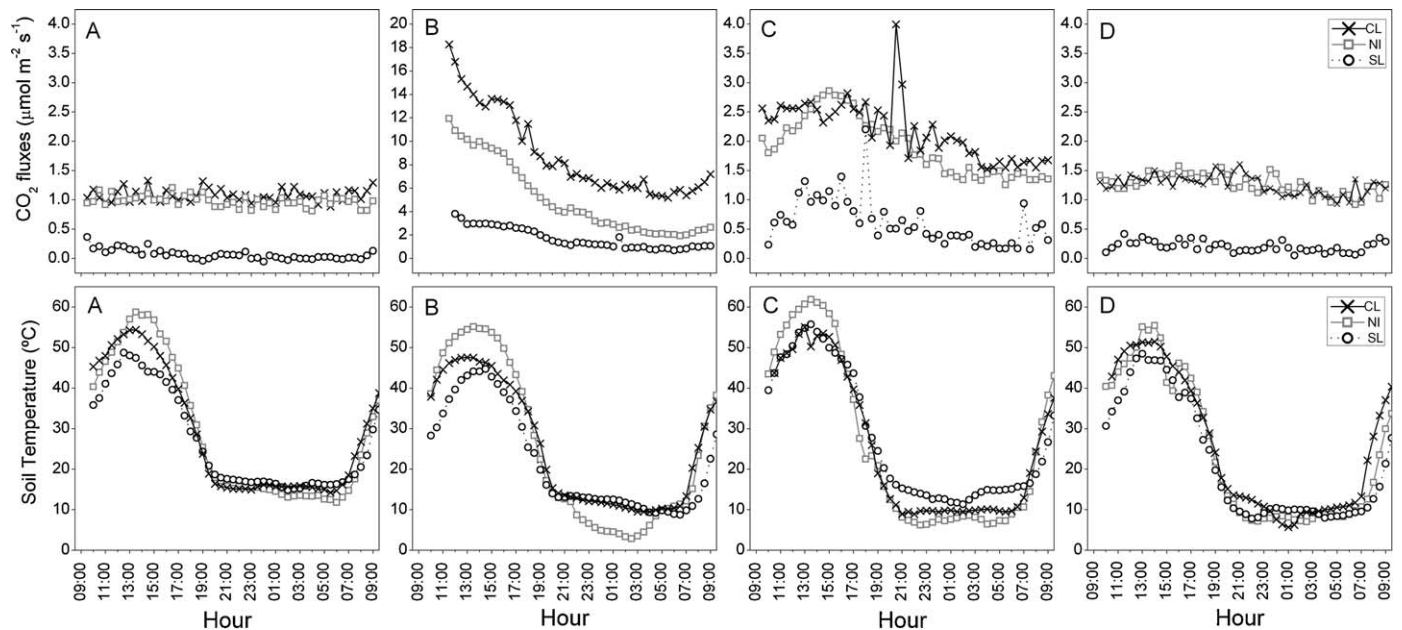


Fig. 5. Half-hourly measurements of soil CO₂ effluxes and soil temperature following the irrigation field experiment in the highest elevation over 24 h. Data from four sampling dates are represented: (A) before irrigation, (B) the day of irrigation, (C) three days after irrigation, and (D) seven days after irrigation. Measurements started at 9:00 am (local hour) and lasted 24 h. CO₂ effluxes measures in (B) from 9:30 to 11:30 am are not shown since they cannot be directly attributed to biological emissions (see Appendix C). CL: cut plus logging; NI: no intervention; SL: salvage logging.

5.1. Effect of soil moisture and temperature

Soil moisture and temperature are the main drivers of soil CO₂ effluxes (Davidson et al., 1998; Lloyd and Taylor, 1994). The combination of these two factors is particularly critical in Mediterranean ecosystems, where high temperature in summer is coupled with limiting soil moisture (Carlyle and Bathan, 1988; Davidson et al., 1998; Reverter et al., 2010; Xu and Qi, 2001). The effect of water availability on respiration was clear in this study as seen both indirectly (correlation with the rewetting index; seasonal variation of CO₂ fluxes, with basal values in summer and maximum values in spring) as well as by experimental manipulation of water availability (see Almagro et al., 2009; Liu et al., 2002; Rey et al., 2002; Xu et al., 2004; for similar results).

The effect of soil temperature was, by contrast, almost irrelevant. This is an expected result for the dry period (summer), when limiting soil moisture overshadows the role of temperature (Carlyle and Bathan, 1988; Davidson et al., 1998; Serrano-Ortiz et al., 2007; Sowerby et al., 2008; Xu and Qi, 2001). This result is reinforced by the restriction of the temperature sensitivity analysis to diurnal measurements at a single collar (per treatment), thus avoiding the potentially confounding and interacting effects of spatial variability, primary productivity and phenology (Curiel-Yuste et al., 2004; Janssens et al., 2001). In any case, soil fluxes at seasonal scales also showed very weak temperature sensitivity during drought conditions (data not shown). However, low values of Q₁₀ were similarly encountered during spring (although slightly higher than in summer), as well as in the controlled irrigation experiment. This contrasts with results in most of the studies for both seasonal and diurnal fluxes in un-burnt Mediterranean climates (Raich and Schlesinger, 1992; Reichstein et al., 2002; Rey et al., 2002; Tang et al., 2003, 2005; Xu and Qi, 2001) and suggests that factors other than water limitation could be restricting the diurnal effect of soil temperature; these might include the repression of the microbial activity by the extremely high temperatures reached in the soil during the midday (Killham, 1994; Luo and Zhou, 2006; Tang et al., 2003) and during the fire (García-Oliva et al., 1999; Saa et al., 1998; Zhang et al., 2005). In addition, heat and CO₂ transport processes can influence Q₁₀ values calculated from regressions of surface flux and soil temperature measured at a single depth (Phillips et al., 2011; Xu and Qi, 2001). Thus, Q₁₀ values could be higher at higher depths.

In any case, soil respiration almost halved at the higher elevation. Several factors can be involved in this pattern including lower rate of wood decomposition, lower primary productivity and subsequent root activity and litter deposition (Brischke and Rapp, 2008; Craine et al., 1998; Janssens et al., 2001; Knapp et al., 1998;), but it is very likely that colder temperatures at higher elevation influence respiration differences between altitudinal levels (Kane et al., 2003), whether directly or via interactions with the above-mentioned factors.

5.2. Effect of burnt wood management

Soil respiration was consistently affected by post-fire burnt wood management both across seasons and altitudinal levels, whatever the effects of moisture and temperature. Overall, respiration was highest in the treatment where trees were felled and lopped, leaving the soil partially covered with logs and branches (CL treatment). This may be explained by several factors. First, the decaying wood may supply the soil with nutrients that encourage microbiological activity (Coleman et al., 2004; Grove, 2003; Harmon et al., 1986). The fact that trees were felled would facilitate wood-soil contact and hence decomposition (Harmon et al., 1986; Maser and Trappe, 1984), explaining the higher respiration rates in CL versus NI. Second, logs and branches spread on the ground

can improve microclimate by reducing soil desiccation produced by the extreme soil heating (Castro et al., 2011; see also Smaill et al., 2008; Stoddard et al., 2008 for similar effects of non-burned woody debris). Third, vegetation cover was consistently higher in collars in CL than in the other treatments, which may increase both autotrophic (either above and belowground) and heterotrophic respiration (Reichstein et al., 2003; Tang et al., 2005). This is likely a consequence of higher nutrient availability and microclimatic amelioration (Burton et al., 2000; Irvine et al., 2007; Stark et al., 2006), but altogether exerted a direct effect on soil respiration during spring.

We are not aware of studies analyzing the effect of post-fire burnt wood management on soil respiration by means of an experimental design with different levels of intervention. However, Concilio et al. (2006) and Irvine et al. (2007) reported an increase in soil respiration following a fire of high intensity due to the presence of slash on the forest floor. In these cases, the increases in soil respiration were attributed to regrowth and nutrient inputs. Burnt wood management alters microclimate, nutrient content or vegetation cover regardless of the ecosystem considered (e.g. Castro et al., 2011; Coleman et al., 2004; Grove, 2003; Harmon et al., 1986; Stoddard et al., 2008). Thus, it is likely that burnt wood would encourage soil microbial activity and respiration rates in the upper soil layers after a wildfire.

5.3. Effect of rain events

In addition to the positive relationship between soil moisture and respiration, this study shows the strong impact of evenly distributed rain events on soil CO₂ effluxes of a Mediterranean ecosystem. The simulation of a summer rain event provoked a CO₂ peak that reached *ca.* 47 times the basal values before the experimental watering. Furthermore, the effects of post-fire treatments are highlighted by the coincident patterns, both in the seasonal measurements of soil respiration and following experimental watering, with the highest values reached in the CL treatment. Vegetation was senescent at the beginning of the irrigation experiment, and no changes in living vegetation cover were observed following irrigation, so the increased soil CO₂ effluxes after the first 2 h of the water addition could be attributed mainly to microbial activity. Thus, differences in soil carbon pools like those due to decaying burnt wood can alter both peak and basal respiration rates (Sanderman et al., 2003).

Our results strongly suggest that a large fraction (about 64% approx.) of the initial CO₂ emitted within *ca.* 2 h after water addition was related to degasification of CO₂-rich air trapped in soil pores. During the dry season, CO₂ from the past and from water-limited metabolism would be trapped in soil pores (Inglis et al., 2009; Liu et al., 2002) when the soil is very dry and the low connectivity of soil pores leads to CO₂ accumulation. After initial soil degassing, rewetting leads to a cascade of responses (enhanced microbial activity and soluble organic C availability; Luo and Zhou, 2006; Xiang et al., 2008) that mobilizes and metabolizes otherwise unavailable soil carbon. This would explain the high peaks and exponential decrease of CO₂ effluxes. Thus, even if differences in soil respiration among treatments were not of a high magnitude during summer, their effect can be cumulative and show up after rain events following a long dry period.

5.4. Management implications

There is currently an intense debate concerning the appropriate management of burnt trees after forest fires (Beschta et al., 2004; Donato et al., 2006; Lindenmayer et al., 2004; McIver and Starr, 2001). Post-fire salvage logging is implemented worldwide (Castro et al., 2011; Lindenmayer et al., 2004; McIver and Starr,

2001; Van Nieuwstadt et al., 2001), but recent studies show that it may impact ecosystem function and regeneration (Castro et al., 2010, 2011; Donato et al., 2006; Lindenmayer and Noss, 2006). The present study highlights the capacity of burnt wood management to alter soil CO₂ effluxes. Overall, salvage logging was the treatment with the lowest soil respiration, probably because of harsher micro-climatic conditions and reduced nutrient availability (see above). Since this pattern was consistent in the two contrasted altitudinal levels of the study, with different dominant tree species before fire disturbance, these results could be extrapolated to other forest ecosystems in water-limited climates.

Post-fire management strategies should also be considered for carbon sequestration policies. Their relevance is accentuated given the increase in wildfire intensity and frequency in recent decades due to human factors (Cerdà and Mataix-Solera, 2009; Conard et al., 2002) and predicted climatic change scenarios (IPCC, 2007). Post-fire wood management can determine the rhythm of natural recovery of the ecosystem and net carbon balance by modifying soil parameters. However, the higher soil respiration reported in the “cut plus lopping” treatment does not necessarily imply an increase in net carbon emissions of the burnt area, but rather can be interpreted as a comparative diagnostic tool for soil metabolic activity in relation to forest practices (Weber, 1990). Primary production can equilibrate increases in CO₂ effluxes (Irvine et al., 2007), since the herbaceous cover registered during spring was higher in this treatment. Furthermore, the effect of burnt logs, branches or coarse woody debris over the soil may be long-lasting (Smaill et al., 2008), helping to compensate ecosystem fluxes over longer time scales. In order to disentangle the role of the burnt wood management on

soil carbon sequestration, complementary studies on ecosystem-atmosphere carbon exchange would be convenient. In any case, this study sets a baseline and is the first that experimentally examines the key importance of post-fire wood management practices on soil CO₂ fluxes.

Acknowledgements

Thanks to Luis Miguel Oviedo and Cécile Lamouroux for their help in the field. Precipitation data were facilitated by Jose Ramón Francia Martínez under the project (RTA2007-00008-00-00) financed by the National Institute of Agrarian Research and Food Technology (INIA) and cofinanced with the FEDER funds of the European Union. We are especially grateful to the Environmental Council (Junta de Andalucía) and to the Natural and National Reserves of Sierra Nevada for support in the establishment of the treatments. This work was financed by the Project SUM2006-00010-00-00 of the INIA, by the Project 10/2005 of the *Organismo Autónomo de Parques Nacionales* (MMA) and by the project GES-BOME (P06-RNM-1890) of the Junta de Andalucía.

Appendix A.

Soil CO₂ effluxes in each sampling date in every treatment and elevation. Mean values of soil fluxes ($\mu\text{mol m}^{-2} \text{s}^{-1}$) are followed by $\pm 1\text{SE}$ ($n = 20$). CL: cut plus lopping; NI: no intervention; SL: salvage logging; HE: high elevation (2317 m a.s.l.); LE: low elevation (1477 m a.s.l.).

Season	Sampling date	Elevation	Treatment		
			CL	NI	SL
Summer 07	05-July	HE	1.19 $\pm$ 0.08	1.31 $\pm$ 0.12	0.97 $\pm$ 0.12
		LE	2.04 $\pm$ 0.16	2.17 $\pm$ 0.22	1.69 $\pm$ 0.16
	19-July	HE	1.07 $\pm$ 0.21	0.71 $\pm$ 0.07	0.76 $\pm$ 0.07
		LE	2.37 $\pm$ 0.30	2.16 $\pm$ 0.25	1.90 $\pm$ 0.28
	2-August	HE	1.10 $\pm$ 0.22	0.60 $\pm$ 0.06	0.75 $\pm$ 0.11
		LE	2.02 $\pm$ 0.25	2.26 $\pm$ 0.30	2.03 $\pm$ 0.23
	30-August	HE	0.88 $\pm$ 0.20	0.52 $\pm$ 0.08	1.12 $\pm$ 0.40
		LE	1.92 $\pm$ 0.19	2.00 $\pm$ 0.29	1.93 $\pm$ 0.32
Autumn 07	25-September	HE	3.87 $\pm$ 0.37	4.27 $\pm$ 0.55	4.85 $\pm$ 0.41
		LE	5.46 $\pm$ 0.30	4.79 $\pm$ 0.50	4.21 $\pm$ 0.26
	30-October	HE	1.92 $\pm$ 0.12	2.00 $\pm$ 0.20	0.83 $\pm$ 0.06
		LE	2.45 $\pm$ 0.21	2.42 $\pm$ 0.33	1.83 $\pm$ 0.15
Spring 08	15-April	HE	2.29 $\pm$ 0.27	2.16 $\pm$ 0.24	0.76 $\pm$ 0.09
		LE	5.22 $\pm$ 0.41	3.98 $\pm$ 0.44	2.86 $\pm$ 0.25
	19-May	HE	3.82 $\pm$ 0.56	3.14 $\pm$ 0.52	2.43 $\pm$ 0.20
		LE	14.92 $\pm$ 1.87	7.38 $\pm$ 1.18	6.57 $\pm$ 1.13
Summer 08	02-September	HE	0.92 $\pm$ 0.14	0.47 $\pm$ 0.05	0.62 $\pm$ 0.09
		LE	2.38 $\pm$ 0.19	2.07 $\pm$ 0.26	1.93 $\pm$ 0.36
Autumn 08	01-October	HE	3.51 $\pm$ 0.34	3.55 $\pm$ 0.41	1.61 $\pm$ 0.14
		LE	7.08 $\pm$ 0.27	4.08 $\pm$ 0.38	4.79 $\pm$ 0.51

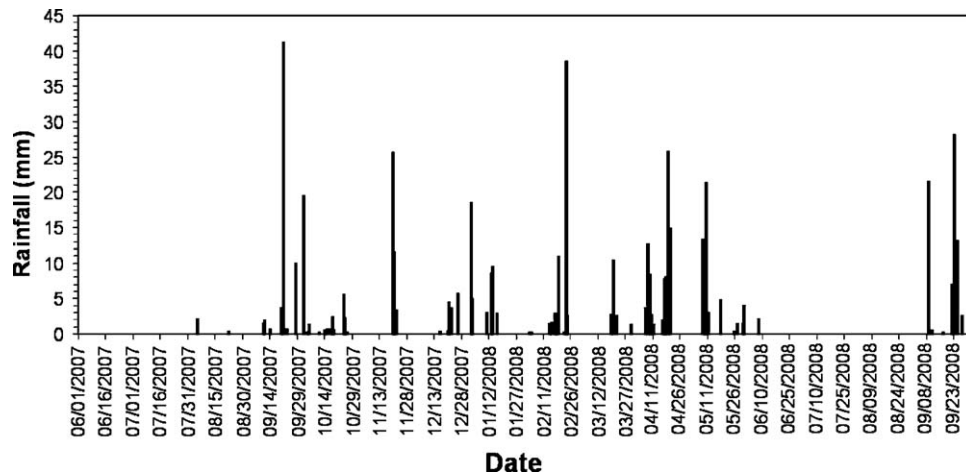


Fig. B1. Rain events during the measurement period. Data from a meteorological station near LE.

Table C1

Exponential decay parameters for post-irrigation declines in soil CO₂ effluxes. CL: cut plus lopping; NI: no intervention; SL: salvage logging.

Treatment	Degassing period (d)		Respiration (r) period	
	$F_{0,d}$ ($\mu\text{mol m}^{-2} \text{s}^{-1}$)	τ_d (h)	$F_{0,r}$ ($\mu\text{mol m}^{-2} \text{s}^{-1}$)	τ_r (h)
CL	86.1	1.1	15.7	19.5
NI	47.0	1.2	13.3	11.1
SL	20.1	1.5	3.9	13.6

Appendix B.

See Fig. B1.

Appendix C. Discrimination between the degassing period and the respiration period in continuous measurements of soil CO₂ fluxes after artificial irrigation.

The continuous CO₂ efflux data during the first 24 h after irrigation consistently revealed two distinct periods, each displaying linear declines when plotted on a logarithmic scale (Fig. 5 of the manuscript) and thus corresponding to exponential decay.

Such linear relations can be expressed generally as

$$y = a + bt$$

where t is the time since irrigation, and the remaining variables correspond to the following assignments in the context of exponential decay:

$$y \rightarrow \ln(F)$$

$$a \rightarrow \ln(F_0)$$

$$b \rightarrow -\frac{1}{\tau}$$

In the above formulae, F is the CO₂ efflux (a function of t), F_0 the initial value (at $t=0$), and τ the time constant describing the exponential decay. These assignments are chosen such that the decline can be expressed as

$$\ln(F) = \ln(F_0) - \frac{1}{\tau}t.$$

When the above equation is equated in terms of the exponent of e (ca. 2.718), an exponential decay is described as

$$F = F_0 \exp^{-(1/\tau)t},$$

where τ is the time required for the flux to fall to ca. 37% (e^{-1}) of its initial value (F_0).

For every treatment, a rapid exponential decay was observed during the first 2 h, after which time a more slowly decaying efflux proceeded. We interpreted these periods as corresponding to two separate processes associated with the irrigation treatment: first, during the first couple of hours, physical degassing (period “ d ”) as soil pores were filled by water (Luo and Zhou, 2006); and later, the decline of respiration (period “ r ”) governed by enzyme kinetics (Inglis et al., 2009; Liu et al., 2002; Xiang et al., 2008) as the soil asymptotically returned to its water-limited state (Fig. 5 of the manuscript). For each period, we determined linear fit parameters (a and b) by least-squares regression, and thereby the parameters F_0 and τ (summarized in Table C1) describing the different exponential decay processes.

The purpose of this analysis was merely to exclude the degassing period and thereby isolate the respiration period (excluding the first couple of hours), in order to explore the effect of soil moisture on biologically determined CO₂ fluxes in the irrigated collars.

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