Disentangling the effects of tree species and microclimate on heterotrophic and autotrophic soil respiration in a Mediterranean ecotone forest

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ABSTRACT

Understanding how forest ecosystems influence the response of soil respiration (R_S) to climate drivers is essential to accurately predict soil carbon dioxide (CO_2) fluxes in a changing environment. This is particularly crucial in areas of contact between coniferous and broadleaved forests in the Mediterranean region which are already experiencing a warmer and drier climate. We present a case study in a Mediterranean ecotone forest where R_S components –heterotrophic (R_H) and autotrophic (R_A)– were monitored beneath pure Scots pine (*Pinus sylvestris* L.) and Pyrenean oak (*Quercus pyrenaica* Willd.) stands using the root-trenching method. We used generalized linear models to predict the soil CO_2 efflux based on interactions between soil water content (SWC) and soil temperature. Regardless of the tree species, we found that the strong and inverse water availability and thermal seasonality of the Mediterranean climate intensely constrained soil microbial activity. The incorporation of the soil temperature-moisture covariation thus greatly improved the quality of the models compared to approaches that consider soil temperature alone. We also identified species-specific responses influencing both the total amount of R_A and its sensitivity to environmental variables. Root respiration in the Scots pine stand showed greater vulnerability to the decline in SWC throughout the summer than in the oak stand. The R_A in the Pyrenean oak stand was mainly limited by low soil temperatures in winter, indicating low maintenance rates during vegetative dormancy. Mean annual R_H rates were highest in the Scots pine stand, probably driven by the larger litterfall rates and soil carbon (C) stocks; however, the apparent turnover rate of soil organic C in the oak stand was almost twice as fast as in the pine stand. While our observations are limited to a case study, our work shows that both soil moisture and forest composition can significantly control the temperature dependence of R_S components under a Mediterranean climate.

1. Introduction

Land cover changes in forests occur to a large extent as a result of climate change and modifications in forest practices (Allen et al., 2010; Peñuelas and Boada, 2003). Alterations in the dominant tree species can significantly alter soil respiration (R_S), which in turn affects the global carbon (C) cycle, since soils are responsible for 60–90% of the carbon dioxide (CO_2) released into the atmosphere in terrestrial ecosystems (Goulden et al., 1996). Soil CO_2 efflux is the outcome of the metabolic processes of plant roots (autotrophic respiration, R_A) and microbial communities (heterotrophic respiration, R_H) (Hanson et al., 2000; Kuzyakov, 2006). It is therefore important to determine the

contribution of each component to R_S and their dependence on climate drivers to gain a deeper insight into the effects of changes in forest composition on soil C cycling and respiration (Barba et al., 2016; Bond-Lamberty et al., 2004a).

It is well known that temperature is the main factor controlling soil metabolic activity, so the kinetics of released CO_2 have usually been modelled by a broad set of temperature-dependent functions (Fang and Moncrieff, 2001; Kirschbaum, 1995; O'Connell, 1990; Tuomi et al., 2008). However, the temporal variability of R_H observed in field experiments captures not only its dependence on soil temperature and resource quality, but also reflects the limitations on decomposition caused by soil water content (SWC) (Chang et al., 2014; Davidson and

Abbreviations: R_S , soil respiration; R_H , heterotrophic respiration; R_A , autotrophic respiration; SWC, soil water content; SWB, soil water balance; WHC, maximum soil water holding capacity; ET_o , daily potential evapotranspiration; P, precipitation; ρ , Spearman's rank correlation; D^2 , explained deviance; DOY, day of year; AICc, corrected Akaike Information Criterion; W_{AIC} , Akaike weights

Janssens, 2006; Lellei-Kovács et al., 2016); e.g. drought restricts substrate availability while excess water slows oxygen diffusion for decay processes. Soil microclimate limitations at the field scale can also cause physiological stress to both microbes and plants, which may display different response behaviours in R_H and R_A (Bond-Lamberty et al., 2004a; Galiano et al., 2011; Manzoni et al., 2014). Studies investigating the combined effects of soil temperature and SWC on R_S components are scarce in Mediterranean and semiarid ecosystems, although both climate drivers may significantly influence soil C efflux (Chang et al., 2014; Lellei-Kovács et al., 2016; Rey et al., 2002; Tedeschi et al., 2006). There is therefore a need for experimental approaches that address the dynamic interaction between soil temperature and SWC in decomposition processes and root activities in order to understand the seasonal variability of R_S in forest ecosystems.

Vegetation also controls R_S and its fractions through its influence on litter quantity and quality, nutrient availability, microbial decomposer community, carbohydrate allocation patterns, root biomass, hydrological processes and surface soil temperatures (Bardgett and Wardle, 2010; Fernández-Alonso et al., 2018; Höglberg et al., 2001; Salomón et al., 2015). On large spatial scales, the length of the plant-growing season is one of the major drivers of R_S (Chang et al., 2014; Goulden et al., 1996) as it regulates the gross primary production of the ecosystems (Reichstein et al., 2003). Gross primary production stimulates the total metabolic activity in the soil through the net primary production, which provides the inputs of above- and belowground litter for microbial decomposition (Chang et al., 2014; Reichstein et al., 2003), and through the fresh photosynthetic products or tree carbohydrate reserves that fuel the metabolic activity of the root systems (Phillips et al., 2016). Variations in seasonal patterns of R_S across species may thus be the result of differences in the response of R_A and R_H to soil microclimate variables (Bond-Lamberty et al., 2004a). These differences in the relative contribution of R_A and R_H to R_S could be particularly significant when comparing vegetation species with differences in leaf longevity such as coniferous and broadleaved forests (Curiel Yuste et al., 2004). It is therefore crucial to study the seasonal evolution of R_A and R_H in each forest type individually in order to improve the forecasts of R_S rates with the predicted changes in species distribution.

The ecotones between conifers and broadleaved species in the Mediterranean basin conform a particularly relevant case where the effects of plant functional traits and environmental constraints on R_S overlap. The contact limit between Scots pine forests (*Pinus sylvestris* L.) and Pyrenean oak forests (*Quercus pyrenainca* Willd.) on the Iberian Peninsula is a representative example of these ecotones. In these sites the Scots pine is located at one of its southernmost geographical distribution limits, and locally in its lowermost altitudinal range (Martínez García and Montero, 2000), hence extreme drought events in the summer can potentially lead to episodes of pine die-off (Allen et al., 2010; Martínez-Vilalta and Piñol, 2002). The ongoing intensification of climate-change-driven drought in southern Europe (Stagge et al., 2017) is aggravating water stress in Scots pine and leading to its replacement

by oak species (Galiano et al., 2010) such as the Pyrenean oak, which is better adapted to physiological drought and continental temperatures (Sánchez Palomares et al., 2008).

A three-year long case study was conducted to subtract *in situ* R_A from R_S using the root-exclusion method (Ewel et al., 1987), and to monitor the soil CO_2 efflux in a specific ecotonal area between Scots pine and Pyrenean oak in the Valsaín mountains (central Iberian Peninsula). We aim to assess how seasonality and environmental conditions influence soil CO_2 efflux depending on the functional composition of the forest (Scots pine vs. Pyrenean oak stands). First, we modelled the interaction between soil temperature and SWC on the R_S components under pine and oak stands. We expected species-dependent effects, since the relevance and role of environmental drivers differ between tree species composition given their contrasting ecological strategies. Second, we used fitted models to predict the daily estimates of R_A and R_H for both tree species from daily soil temperature and SWC. Third, we calculated annual cumulative R_H fluxes and compared the apparent soil C turnover rate in both forest types. We hypothesized that annual R_H would be greatest in the pine stand, coinciding with the substantial amount of C stored in this soil as shown in previous studies. We further hypothesized that soil C turnover would be higher in the oak soil since soil organic matter is believed to be more stable in pine stands.

2. Material and methods

2.1. Study site

This study was conducted in the Valsaín forests (40° 51' N, 4° 3' W, ETRS89) located on the north-western slopes of the Sierra de Guadarrama National Park (Central Range, Spain). The study area is at an altitude of about 1350 m a.s.l., where both Pyrenean oak and Scots pine stands are common. The mean annual temperature was 11.0 °C and the mean annual precipitation 621 mm for the study period (Embalse del Pontón Alto weather station, National Meteorological Agency, 9 km away from the experimental sites). Soils are shallow and acidic (pH values in KCl of 4.3 and 5.1 in topsoils under pine and oak respectively (Díaz-Pinés et al., 2011b)) and are Humic Cambisols (Soil Survey Staff, 2014) with sandy loam texture developed on siliceous bedrock, mostly granite and gneiss.

We selected two monospecific forests of Scots pine and Pyrenean oak that were representative in terms of past and current management –oak coppicing for charcoal and pine shelterwood for timber production– on stand structures in the Guadarrama Range, with limited environmental confounding factors (e.g. slope, altitude, bedrock and climate) since they were 1400 m apart. Soil organic matter content varied widely between the forests, especially in the upper soil layers (Table 1), resulting in a stock of 40.6 Mg C ha⁻¹ in the oak stand and 91.7 Mg C ha⁻¹ in the pine stand (forest floor and 0–50 cm of mineral soil (Díaz-Pinés et al., 2011b)). The Scots pine stand is managed under a

Table 1

Soil parameters required to calculate soil water holding capacity (WHC) in each forest stand. Compiled with data from Díaz-Pinés et al. (2011b) and methodology from Gandullo (1994). SOM: Soil organic matter content.

Tree species	Slope	Depth (cm)	Clay (%)	Silt (%)	SOM (%)	Fine-earth (< 2 mm)	WHC (mm H ₂ O m ⁻¹ depth)
Oak	0.18	0–5	4	43	3.9	73	27.3
		5–10	4	45	1.8	71	24.2
		10–20	12	27	1.0	75	45.7
		20–30	10	28	0.8	75	43.5
		0–30					140.7
Pine	0.21	0–5	10	32	12.8	73	40.5
		5–10	12	28	5.5	74	29.7
		10–20	14	27	2.4	74	51.4
		20–30	14	26	2.1	74	49.6
		0–30					171.2

uniform shelterwood system. The Pyrenean oak stand has traditionally been coppiced since the 12th century (Ximénez de Embún, 1977), although this practice was abandoned in the 1970s. The oak stand has around 60-year old stems, 17.2 m² ha⁻¹ basal area, 932 stems ha⁻¹ and 9.7 m mean height; the pine stand has about 80-year old trees, basal area of 64.3 m² ha⁻¹, 718 trees ha⁻¹ and 19 m mean tree height (Díaz-Pinés et al., 2011b).

2.2. Experimental design

The root-trenching method was used to measure *in situ* R_H and R_S following the protocol of Hanson et al. (2000). In January 2014, we established two different rooting treatments, designated as ‘control’ and ‘root-exclusion’, with four replicated plots each (1 m × 1 m) inside each forest stand at a distance of less than 2.5 m from the tree stems and with a mean distance of 30 m between the same treatment plots. In the root-exclusion treatment, we dug a ditch around the plot boundaries to physically isolate the soil matrix from the tree root system. A trench 40-cm deep was considered sufficient to gauge the extent of the effective root depth, since the soil depth ranges from 20 to 50–60 cm, and most of the roots are in the uppermost 15–20 cm of the soil profile. An anti-root geotextile was then placed vertically in the ditch and the outer part of the ditch was refilled with the previously extracted soil material. The surface was periodically clipped to ensure that herbs did not develop inside the trenched plots. Control plots –without the excision of roots– served to monitor R_S . In the root-exclusion treatment it was assumed that R_A was completely suppressed and hence solely R_H occurred –i.e. CO₂ efflux derived from the microbial decomposition of soil organic matter and plant litter (Kuzakov, 2006). The term R_A refers to root-derived CO₂ but may also comprise contributions from rhizomicrobial respiration from mycorrhizal fungi (Bond-Lamberty et al., 2004a; Kuzakov, 2006).

2.3. Soil CO₂ efflux measurements

Two polyvinylchloride respiratory collars (20 cm in diameter) were inserted to a depth of 2 cm in the mineral soil in each plot. A four-month period was allowed to elapse before beginning soil respiration measurements in order to reduce the overestimation of R_H while the severed pre-existing roots were decaying (Butler et al., 2012; Hanson et al., 2000). The 32 respiratory collars (2 forest types × 2 treatments × 4 replicated plots × 2 respiratory collars) were monitored for soil CO₂ efflux on a monthly basis from April 2014 to April 2017 (35 measurement campaigns). The influence of additional C efflux from old root decomposition in our field-registered values should be minimal, since the measurements presented here lasted three years (Díaz-Pinés et al., 2010). Manual measurements of soil CO₂ efflux were taken using a non-steady-state through-flow chamber (Pumpanen et al., 2004). The respiratory collars were closed with a self-made chamber lid (10 cm height and 4.04 l volume) equipped with a rubber septum in the top where a stainless-steel needle vent was inserted to avoid overpressure and disturbing the CO₂ diffusion from the soil into the chamber headspace (Hutchinson and Livingston, 2001). The respiratory chamber was also fitted with outlet and inlet Teflon tubes (2.5 mm inner diameter) coupled to a portable infrared gas analyser WMA-4 (PP Systems, Hertfordshire, United Kingdom). A pump circulated the air through the closed-path system at a constant rate of 0.5 l min⁻¹ during the closed-chamber period (5 min). The headspace CO₂ concentration was recorded from one minute after the chamber closure to discard fluctuations immediately after the lid onset at 30-s measurement intervals. Soil respiration rates were calculated as the linear increase in CO₂ concentration in the time after the chamber closure, considering chamber volume, soil area, air temperature and air pressure, and expressed as mg CO₂-C m⁻² h⁻¹. No signs of flattening of the CO₂ concentration in the headspace were observed throughout the closure time. The portable analyser was calibrated prior to the sampling events using 400 µL L⁻¹

of standard CO₂ gas (Air Liquide, Madrid, Spain) under ambient air pressure. Soil respiration was measured between 07:30 and 16:30 h (local time). Although diel patterns are unlikely to occur in closed canopy stands, special care was taken to fully randomize the sampling sequence across plots in each measurement campaign to account for potential diel fluctuations. Average soil CO₂ efflux at the plot level was computed for each measurement campaign to avoid within-group correlation in the statistical models during data analysis (n = 2 respiratory collars).

During the soil CO₂ efflux measurement campaigns, air and soil temperature and volumetric SWC were measured on the individual plots using probes, a Termistor Vertix 5989M (Herter Instruments, Barcelona, Spain) and a time-domain reflectometer (Field Scout TDR 100, Spectrum Technologies Inc., Aurora, IL, USA) respectively. Soil temperature was recorded on an hourly basis by means of three sensors randomly installed in each forest stand (DS1922L ThermoChron, iButtonLink LCC, Whitewater, WI, USA). Soil temperature and SWC were measured at 10 cm depth in the mineral soil.

The root-exclusion treatment disrupts the root water uptake and may therefore produce disturbances in the soil water regime (Díaz-Pinés et al., 2010; Hanson et al., 2000). In order to avoid potential bias on measured CO₂ efflux caused by altered SWC in the trenched plots, we modelled the response surfaces of both R_S and R_H to the interaction effects between soil temperature and moisture measured in each sampling event (see data analysis in Section 2.5.). We subsequently used the fitted models to predict soil CO₂ efflux throughout the study period using corrected values of daily SWC calculated with a soil water balance (SWB) model.

2.4. Soil water balance for estimating soil water content

The daily SWC during the study period was estimated with a SWB model (Thorntwaite and Mather, 1955). The input variables for the model were: potential evapotranspiration (ET_o), maximum soil water holding capacity (WHC) and precipitation (P) in both forest stands. The model assumes that the depletion of SWC occurs exponentially on dry days when P < ET_o, whereas there is a direct increase in SWC on humid days when P > ET_o (Botey et al., 2011). The ET_o was calculated according to the modified equation of Penman-Monteith (Allen et al., 1998), based on meteorological variables registered at a nearby weather station (Embalse del Pontón Alto). Given that soil forests may present irregular properties at depth, the WHC was calculated from texture, organic matter content, slope and permeability of soil layers at different soil depths (0–10, 0–20, 0–30 and 0–50 cm) following the physical model proposed by Gandullo (1994) (see also Domingo et al., 2006). The SWB was calculated from January 2014 (four months before the start of soil CO₂ measurements) coinciding with water-saturated conditions (SWC = WHC) in soils, as is common in winter in both forests. After initializing the SWB model for 4 months, we assumed the values predicted for daily SWCs were already adjusted to current field conditions at the onset of the soil CO₂ measurements. Estimated SWCs calculated with the WHC for soil properties in the first 30-cm of soil (Table 1) gave the best coefficients of determination with measured SWCs using the TDR probe (R^2 = 0.77 and 0.79 in oak and pine forest stands respectively; p-value < 0.001).

2.5. Data analysis

Differences in soil temperature and SWC across seasons both within and between tree species were evaluated separately with the non-parametric Kruskal-Wallis test, using Dunn’s test for pairwise comparisons of mean rank sums (PMCR package, Pohlert, 2015). Annual and seasonal differences in soil microclimate variables between treatments were also assessed using the non-parametric Kruskal-Wallis test. Spearman’s rank correlation (ρ) was performed between soil temperature and SWC for each forest stand. Seasonal delimitations were

established according to their astronomical definition (March 21st, June 21st, September 21st and December 21st) since they fit the seasonal fluctuations of soil microclimate conditions.

We used generalized linear models with gamma error distribution to relate soil CO₂ efflux to soil temperature, SWC and treatment (*stats* package (R Core Team, 2017)). An individual model was built for each forest to account for differences in the relationships between R_S components and soil microclimate. We tested two biological responses as a function of soil temperature: (1) an exponential increase in R_S components—biological activity increases without any limit—; and (2) a second-order exponential growth of R_S components according to the Gaussian function (O’Connell, 1990)—R_S reaches its maximum at a given temperature, above which it declines with any further increases in soil temperature. We used the logarithmic link function in the models to linearize the exponential relationship between R_S and the independent variables. We included the categorical variable Treatment and its interaction terms with all the independent variables in the model formulations. We fitted additional generalized linear models to examine the potential interactive effects between SWC and soil temperature on R_S components. We introduced the SWC as either first- or second-order exponential functions. The combination of the two temperature-dependence functions with no effect, a linear effect or a quadratic effect of SWC resulted in six separate fitted models for each forest (Table 3).

In a second step, we compared the performance of the models in terms of the reduction in the corrected Akaike Information Criterion (AICc) (Akaike, 1973; Burnham and Anderson, 2002). The models were selected by calculating the Akaike weights (W_{AIC}) (Johnson and Omland, 2004) based on two sets of candidates (Lellei-Kovács et al., 2016): models that considered only temperature-dependence functions, and the six models together. The confidence set of best candidate models for the observed data included all the models with a W_{AIC} within 10% of the highest. We examined the explained deviance (D^2) and the significance of each fitted coefficient in the model selected. An iterative process of stepwise removal of the least important terms was performed to select the optimal reduced model. The procedure was repeated until only significant coefficients remained in the model (Table 4, $p \leq 0.1$). After each step, we inspected the D^2 , the normal probability plot and the residual plot against the predicted values for the fitted models. We also examined the residual variability against the explanatory variables and the plots, and considered them to be a qualitative factor since measurements of soil CO₂ efflux were repeated on the same plots throughout the study. Residual heterogeneities were similar between plots in the fitted models, and we therefore assumed that the variation was ecologically irrelevant and do not consider plots as a random factor in the models (Bolker, 2008).

The optimal reduced models were used to estimate daily R_S and R_H for the whole study period (April 2014–April 2017) and thus to correct any possible bias introduced on the measured soil CO₂ efflux by the higher SWC in root-exclusion plots. We used the daily average soil temperature (registered with the iButton sensors) and daily SWC (estimated by means of the SWB in Section 2.4) as input data for the models. Daily rates of R_A were calculated by subtracting modelled R_H

from modelled R_S. We aggregated the daily values of the R_S components to obtain cumulative seasonal and cumulative annual estimates, and calculated the average values for each day of the year (DOY: 0–365 days, $n = 3$ growing seasons). We then estimated the mean relative contribution of R_H to R_S throughout DOYs. We also calculated the turnover rate for the soil C as the annual amount of R_H per unit of C stored in the forest floor, plus 0–50 cm of mineral soil (Metcalf et al., 2007; Olsen and Van Miegroet, 2010).

Annual and seasonal amounts of R_S, R_H and R_A were tested for differences between tree species using linear models (*stats* package, R Core Team, 2017). Linear models were also applied to test for differences in R_S components across seasons for each tree species. Normality and homogeneity of residuals for the linear fitted models were checked by the Shapiro-Wilk and Levene test (*car* package, Fox and Weisberg, 2011) respectively. Multiple comparisons between the means of the factor levels were made using Tukey’s post hoc analyses.

All analyses were performed in the statistical platform R version 3.4.0. (R Core Team, 2017). The *ggplot2* package (Wickham, 2009) was used to generate 2D general plots, and 3D plots were created with the *lattice* package (Sarkar, 2008).

3. Results

3.1. Variability of soil microclimate and soil CO₂ efflux throughout the study period

Soil microclimate variables at the study site showed pronounced seasonal fluctuations typical of the Mediterranean climate (Fig. 1). Measured soil temperature and SWC had opposing seasonal patterns and hence were negatively correlated ($\rho = -0.85$ and $\rho = -0.73$ in Scots pine and Pyrenean oak forests respectively, p -value < 0.001). The SWC in both forests peaked in mid-winter (Fig. 1b), and then underwent a progressive decrease in spring until reaching its minimum value for the year with the onset of the free-rain period in July, when it remained low until October. Soil water content increased progressively with the start of the autumn rainfall until the soil moisture reached the WHC in winter in both forests. Soil temperature increased in spring (Fig. 1a), peaked around July and then gradually decreased in autumn, and remained low all winter. On the study site, annual average soil temperature was 11.8 ± 0.7 °C and annual average SWC was $8.2 \pm 1.6\%$, without any differences between tree species. With regard to seasons, in winter, soil temperature was higher in the pine than in the oak stand, whereas the opposite occurred in spring (Table 2). The SWC during the winter was higher in the oak than in the pine stand (Table 2). The effect of the root-exclusion treatment on the SWC was only significant in the Scots pine forest (Table 2), which showed higher SWCs in trenched plots than in control plots.

Soil respiration rates varied between forest types and showed large seasonal dynamics, from minimum values in winter to maximum values in spring (Fig. 2a). Soil respiration ranged from 49.0 to 494.8 mg CO₂-C m⁻² h⁻¹ in pine and 35.4 to 572.1 mg CO₂-C m⁻² h⁻¹ in oak stands. Measured R_H showed a similar seasonal pattern to R_S with average

Table 2

Mean $\pm$ standard deviations of hourly values of soil temperature (T, $n = 3$) and soil water content (SWC, $n = 4$) in both forests. Different lowercase letters denote significant differences in average values across seasons within the same tree species, while capital letters denote significant differences between tree species within the same season (Kruskal-Wallis, $p < 0.05$). Asterisks indicate significant differences in the SWC between control and root-exclusion treatment (Kruskal-Wallis, $p < 0.05$).

Soil variables	Forest	Treatment	Winter		Spring		Summer		Autumn		Annual	
T (°C)	Pine	–	4.7 $\pm$ 0.9	A d	11.8 $\pm$ 0.7	B b	18.4 $\pm$ 1.1	a	9.8 $\pm$ 0.4	c	11.7 $\pm$ 0.7	
	Oak	–	3.9 $\pm$ 1.2	B d	13.3 $\pm$ 0.8	A b	18.4 $\pm$ 0.6	a	10.0 $\pm$ 0.5	c	11.9 $\pm$ 0.9	
SWC (%)	Pine	Control	11.4 $\pm$ 2.3	B a	10.6 $\pm$ 3.5	a	2.1 $\pm$ 1.0 [*] b		8.7 $\pm$ 1.7	a	7.7 $\pm$ 2.1 [*]	
		Root-exclusion	12.3 $\pm$ 2.2	a	12.5 $\pm$ 2.1	a	4.5 $\pm$ 0.7 [*]	A c	9.2 $\pm$ 2.2	b	9.3 $\pm$ 1.6 [*]	
	Oak	Control	13.5 $\pm$ 1.4	A a	10.2 $\pm$ 1.5	b	2.7 $\pm$ 0.6	c	10.3 $\pm$ 0.8	b	8.7 $\pm$ 1.0	
		Root-exclusion	13.6 $\pm$ 0.4	a	10.2 $\pm$ 1.9	b	3.3 $\pm$ 1.0	B c	10.8 $\pm$ 1.1	b	9.0 $\pm$ 1.1	

Table 3

Results of model comparisons in (a) Scots pine forest and (b) Pyrenean oak forest. The W_{AIC} of the best candidate models are shown in bold. Arrows indicate the models selected for each tree species. T: daily soil temperature, Tto: treatment (control, root-exclusion), SWC: daily soil water content. Res. dev.: residual deviance, AICc: corrected Akaike information criterion, d.f.: degrees of freedom, D^2 : deviance explained, W_{AIC} : Akaike weights.

Tree species	Generalized linear models		Res. dev.	AICc	d.f.	D^2 (%)	W_{AIC}	
(a) Scots pine	<i>Null</i> ~ 1		64.05	2830.1	254			
SWC is not considered								
Linear effect of T	$T \times Tto$	(1)	52.66	2784.4	251	17.78	< 0.01	< 0.01
Quadratic effect of T	$T \times Tto + T^2 \times Tto$	(2)	42.97	2735.1	249	32.92	1.000	< 0.01
Linear SWC interaction effect								
Linear effect of T	$T \times Tto \times SWC$	(3)	23.47	2581.8	247	63.37	–	0.196
Quadratic effect of T	$T \times Tto \times SWC + T^2 \times Tto \times SWC$	(4)	22.60	2580.5	243	64.77	–	0.391
Quadratic SWC interaction effect								
Linear effect of T	$T \times Tto \times SWC + T \times Tto \times SWC^2$	(5)	22.81	2583.2	243	64.69	–	0.099
→ Quadratic effect of T	$T \times Tto \times SWC + T^2 \times Tto \times SWC + T \times Tto \times SWC^2 + T^2 \times Tto \times SWC^2$	(6)	21.45	2580.9	237	66.51	–	0.314
(b) Pyrenean oak	<i>Null</i> ~ 1		82.83	3081.7	278			
SWC is not considered								
Linear effect of T	$T \times Tto$	(1)	62.88	3007.7	275	24.08	< 0.01	< 0.01
Quadratic effect of T	$T \times Tto + T^2 \times Tto$	(2)	45.11	2916.2	273	45.54	1.000	< 0.01
Linear SWC interaction effect								
Linear effect of T	$T \times Tto \times SWC$	(3)	35.44	2851.6	271	57.21	–	< 0.01
→ Quadratic effect of T	$T \times Tto \times SWC + T^2 \times Tto \times SWC$	(4)	29.41	2807.1	267	64.50	–	0.997
Quadratic SWC interaction effect								
Linear effect of T	$T \times Tto \times SWC + T \times Tto \times SWC^2$	(5)	32.78	2838.0	267	60.43	–	< 0.01
Quadratic effect of T	$T \times Tto \times SWC + T^2 \times Tto \times SWC + T \times Tto \times SWC^2 + T^2 \times Tto \times SWC^2$	(6)	29.23	2818.9	261	64.71	–	< 0.01

values during the measurement period of $138.8 \pm 5.3 \text{ mg CO}_2\text{-C m}^{-2} \text{ h}^{-1}$ in pine and $106.8 \pm 13.5 \text{ mg CO}_2\text{-C m}^{-2} \text{ h}^{-1}$ in oak forests (Fig. 2b).

3.2. Choosing the statistical model for soil CO_2 efflux in each forest

In both forests, the quadratic temperature dependence of soil CO_2 efflux was shown unambiguously to be the model that best fitted the empirical data when considering this climate variable exclusively (Table 3), meaning that increased soil temperatures above an optimum temperature resulted in lower soil CO_2 efflux.

The models that included the interactive effects of soil temperature and SWC on soil CO_2 efflux greatly improved the quality of fit, as seen from the lower AICc values in comparison with models that do not consider SWC (Table 3). In the Pyrenean oak forest, the model for the interaction effect between linear SWC and quadratic soil temperature (model 4 in Table 3b) unequivocally showed the best fit ($W_{AIC} > 0.99$), while in the Scots pine forest all models with interactive SWC effects performed equally, irrespective of the relationship between soil temperature and SWC ($W_{AIC} > 0.01$). In most cases, the model choice strongly affected the predicted values of soil CO_2 efflux at the extremes of the ranges of the data set used in the model fitting procedure (Bond-Lamberty et al., 2004a). The values near the range limits of the soil microclimate variables are normally underrepresented in the data and this may hamper the detection of differences in the shape of the model under these circumstances. We chose the model containing the quadratic interaction effect of soil temperature and SWC to explain soil CO_2 efflux in pine forests (model 6 in Table 3a) because it showed the narrowest confidence intervals with the soil at both its WHC in winter and its wilting point in the free-rain period (data not shown).

Optimal reduced models with all terms statistically significant at $p < 0.1$ for Scots pine and Pyrenean oak forests accounted for 64.8% and 63.7% of the variability in soil CO_2 efflux respectively (Table 4). The main effects of soil temperature explained most of the D^2 in the models of both forest stands (32.4% in pine and 31% in oak). The interaction effects between soil temperature and either SWC or Treatment in the oak stand suggest that optimal temperatures for soil CO_2 efflux vary differently with diverse levels of SWC in R_H and R_A components (Fig. 3b, d and f). The main effects of SWC explained less D^2 in the pine

(6.2%) than in the oak stand (14.7%). We only found an optimal SWC for soil CO_2 efflux in the pine stand, which was also dependent on soil temperature since the interaction effects between both microclimate variables significantly accounted for 2.4% of the model D^2 (Table 4a). The SWC sensitivity of soil CO_2 efflux varied between treatments in the pine stand (Table 4a), indicating both a restriction of R_H above the soil WHC (Fig. 3c), and a restriction on R_A at the soil wilting point (Fig. 3e).

3.3. Soil respiratory components: annual and seasonal patterns

Estimated daily rates of R_A throughout the study period differed between forest types and underwent strong seasonal fluctuations, revealing marked variations between the forests (Fig. 4). R_A ranged from almost negligible values in both stands to 47.6 and 65.9 $\text{mg CO}_2\text{-C m}^{-2} \text{ h}^{-1}$ in pine and oak respectively. R_H followed similar patterns in soils from pine and oak stands (Fig. 4) with minimum rates in winter (52.3 and 35.4 $\text{mg CO}_2\text{-C m}^{-2} \text{ h}^{-1}$ respectively) and maximum rates in late spring (246.5 and 161.8 $\text{mg CO}_2\text{-C m}^{-2} \text{ h}^{-1}$ respectively). The relative contribution of each soil respiratory component to R_S varied throughout the year (Fig. 5). The highest contribution of R_A to R_S in the pine forest occurred in the period between mid-October (DOY 281) and end June (DOY 183), while R_A had a greater relative importance in the oak forest from April (DOY 83) to October (DOY 330).

For the study period (April 2014–April 2017), annual predicted R_S was similar in the Pyrenean oak and Scots pine forests ($p = 0.125$, Table 5). R_A was significantly higher in the oak than in the pine stand ($p < 0.001$), whereas the opposite occurred for R_H , which showed lower values in the oak than in the pine stand ($p < 0.01$). However, the R_H for the stored C in the soils in the study (Díaz-Pinés et al., 2011b) pointed to a significantly faster turnover rate of soil C in the oak than in the pine forest ($p < 0.001$). On average, R_H accounted for 88.2% of total R_S in pine and 75.8% in oak stands.

4. Discussion

4.1. Modelling soil microclimate control on soil CO_2 efflux

Estimates of annual R_S in this study were $1.03 \text{ kg CO}_2\text{-C m}^{-2} \text{ year}^{-1}$ irrespective of the tree species, which is similar to reported values for

Table 4

Parameter estimates of optimal reduced generalized linear models for (a) Scots pine and (b) Pyrenean oak forest. AICc: corrected Akaike information criterion, D²: deviance explained, d.f.: degrees of freedom, SE: standard error, Sign.: significance codes (*** p < 0.001, ** p < 0.01, * p < 0.05, · p < 0.1). Explanatory variables (T: soil temperature, SWC: soil water content).

Terms	AICc	D ²	d.f.	Deviance	Estimate	SE	t-value	Sign.
(a) Scots pine model								
Intercept	2578.3	64.79	244					
Treatment		0.00	254	0.00	3.25	$4.10 \cdot 10^{-1}$	7.92	***
T		0.13	253	0.08	$-2.11 \cdot 10^{-2}$	$7.72 \cdot 10^{-2}$	-0.27	
SWC		42.17	252	26.93	$1.61 \cdot 10^{-1}$	$5.46 \cdot 10^{-2}$	2.95	**
T ²		48.25	251	3.89	$1.23 \cdot 10^{-1}$	$6.79 \cdot 10^{-2}$	1.82	·
SWC ²		56.77	250	5.46	$-4.85 \cdot 10^{-3}$	$1.75 \cdot 10^{-3}$	-2.77	**
SWC × Treatment		60.32	249	2.27	$-4.65 \cdot 10^{-3}$	$3.07 \cdot 10^{-3}$	-1.51	
SWC × control		60.99	248	0.43	–	–	–	
SWC × root-exclusion					$-1.22 \cdot 10^{-2}$	$7.46 \cdot 10^{-3}$	-1.63	·
T × SWC		63.07	247	1.33	$-1.73 \cdot 10^{-2}$	$1.04 \cdot 10^{-2}$	-1.67	·
T ² × SWC		64.14	245	0.68	$1.06 \cdot 10^{-3}$	$4.01 \cdot 10^{-4}$	2.64	**
T × SWC ²		64.16	245	0.02	$1.01 \cdot 10^{-3}$	$5.52 \cdot 10^{-4}$	1.83	·
T ² × SWC ²		64.79	244	0.40	$-5.18 \cdot 10^{-5}$	$2.53 \cdot 10^{-5}$	-2.05	*
(b) Pyrenean oak model								
Intercept	2804.76	63.72	271					
Treatment		0.00	278	0.00	2.81	$1.71 \cdot 10^{-1}$	16.42	***
T		7.36	277	6.10	$8.14 \cdot 10^{-2}$	$1.48 \cdot 10^{-1}$	0.55	
SWC		23.71	276	13.54	$2.24 \cdot 10^{-1}$	$2.38 \cdot 10^{-2}$	9.41	***
T ²		41.41	275	14.66	$4.40 \cdot 10^{-2}$	$6.64 \cdot 10^{-3}$	6.63	***
T × Treatment		62.49	274	17.46	$-6.21 \cdot 10^{-3}$	$8.74 \cdot 10^{-4}$	-7.11	***
T × control		62.89	273	0.33	–	–	–	
T × root-exclusion					$-5.68 \cdot 10^{-2}$	$2.66 \cdot 10^{-2}$	-2.13	*
T ² × Treatment		63.38	272	0.41	–	–	–	
T ² × control					$1.90 \cdot 10^{-3}$	$1.05 \cdot 10^{-3}$	1.81	·
T ² × root-exclusion					$5.30 \cdot 10^{-5}$	$3.29 \cdot 10^{-5}$	1.61	·
T ² × SWC		63.72	271	0.28				

other pine and oak forests in the Mediterranean basin (Barba et al., 2016; Rey et al., 2002). However, our results clearly showed that tree species largely controlled the temporal dynamics of the soil CO₂ efflux in the ecotone through specific responses of R_A and R_H to soil microclimate conditions. We were also able to detect common patterns in the response of CO₂ efflux to the environmental conditions, which can be attributed to the particular climate characteristics of the Mediterranean region. Soil temperature in both forests was largely the best predictor of soil CO₂ efflux; however the inclusion of the soil temperature-SWC covariation critically improved our modelling capability in this drought-prone ecotone.

Independently of the tree species, a strong seasonality of modelled R_S was observed, suggesting an apparent limitation to soil metabolic activity all year round except in spring, the only period when optimal soil temperatures and SWC occur simultaneously. The pattern observed in R_S may be basically explained by the temporal variability of R_H, since it accounted for more than 70% of the total R_S in both forest stands. We also observed peaks of modelled R_H in autumn produced by occasional rainfall events at the beginning of the wet season (Almagro et al., 2009), when temperatures are still warm. This seasonal pattern for R_H in our study has been previously reported in other forests in the Mediterranean basin (Chang et al., 2014; Lellei-Kovács et al., 2016; Rey et al., 2002; Tedeschi et al., 2006). We identified low winter temperatures and low summer SWCs as important climate constraints that dampen the apparent temperature sensitivity of R_H and other factors that stimulate microbial decomposition, such as the timing of leaf and needle fall when there is an extra input of fresh organic matter (Saiz et al., 2007) and/or high-quality litter (Raich and Tufekcioglu, 2000).

Our results also suggest a higher sensitivity of R_A to low values of SWC in pine stands, which agrees with the known vulnerability of Scots pine to drought events (Sabaté et al., 2002; Vayreda et al., 2012). The low SWC values observed here are probably a combined result of the strong seasonality of the precipitation and the low WHC of these coarse-textured soils. High sand contents are common in large areas of the Iberian Peninsula (Ballabio et al., 2016) so we presume these

respiratory patterns are occurring in other Scots pine and Pyrenean oak forests. However, additional case studies specifically addressing a broad range of soil textures are highly recommended to assess the extent of the effects of drought on R_A and R_H at the regional level.

4.2. Seasonal patterns of soil respiration components modulated by tree species composition

Although annual R_A made a modest contribution to total soil CO₂ efflux in our study (12–24%), the differences in this component likely balanced out those of R_H, so similar annual R_S were found in both forest types. Two mechanisms are proposed to explain these differences in R_A: (1) the different root-to-shoot ratios derived from historical management (0.54–0.96 in Pyrenean oak coppices (Salomón et al., 2016a) vs 0.28 in Scots pine forests (Ruiz-Peinado et al., 2011)); and (2) the fact that physiological activity (including roots) is more severely constrained in pine than oak during the dry season, resulting in higher R_A rates in the Pyrenean oak stands. The R_A accounted for 24% of R_S in the Pyrenean oak forest, similar to other oak coppices under a Mediterranean climate (Rey et al., 2002; Tedeschi et al., 2006). The 12% annual contribution of R_A to R_S in Scots pine is also similar to data from old conifer stands in boreal forests (Bond-Lamberty et al., 2004a), but considerably lower than the 36% contribution reported for Scots pine suffering die-off on the north-eastern Iberian Peninsula (Barba et al., 2016), or estimates from warm temperate forests (Bond-Lamberty et al., 2004b). The R_A contribution in both forests falls within the lowest values reported in previous research, which varied from 10% to 90% across vegetation types according to Hanson et al. (2000). To the best of our knowledge, our results for pine are among the lowest estimates in forest ecosystems, which may be due to the low volumetric SWCs (rarely above 14%) which appear to have a more marked effect on R_A than on R_H.

The seasonal patterns for R_A were also significantly different depending on tree species. Water availability has been reported in previous research as a limiting resource for Scots pine growth in

Fig. 1. Seasonal evolution (SP: spring, SU: summer, AU: autumn and WI: winter) of environmental variables throughout the study period (April 2014–April 2017). (a) Daily soil temperature (average values for each forest stand from data collected with iButton sensors at 10 cm in the mineral soil, $n = 3$). (b) Daily soil water content (points represent average values ($n = 4$) for each forest stand with bars indicating standard deviation from data collected with a TDR probe at control plots during measurement campaigns; lines represent daily estimated values from soil water balances (SWB)). (c) Daily precipitation (registered in the nearby weather station, Embalse del Pontón Alto).

Mediterranean climates, mainly at its lowest elevations (Bogino et al., 2009; Camarero et al., 2010; Sánchez-Salguero et al., 2015), which is consistent with the pattern of pine R_A throughout the year. High and sustained R_A rates occurred for pine whenever water was available even outside its growing season (Camarero et al., 2010). Rates of R_A in winter declined by only 20% compared to rates in spring, probably because winter photosynthesis enables the pine to produce and accumulate carbohydrates during this unfavourable season (Sánchez-Salguero et al., 2015). Since SWC in winter was close to WHC, the soil temperature was the constraining factor for pine physiological activity

as shown by the R_A . Warm winters therefore appeared to promote higher rates of root physiological activity, and presumably have a positive effect on pine growth (Bogino et al., 2009). In early spring the warmer temperatures and high SWCs resulted in maximum rates of R_A , coinciding with the resumption of growth in the pines (Camarero et al., 2010). The seasonal trend in R_A then reached a turning point and showed minimum rates in summer, a period with overlapping soil water deficit and high evaporative demand. These minimum R_A rates are consistent with other ecophysiological responses observed in pine trees under summer drought, such as efficient stomatal closure to reduce

Fig. 2. Soil CO₂ efflux measured over the 35 measurement campaigns in (a) the control plots (R_s : total soil respiration); and (b) the plots with root-exclusion treatment (R_H : heterotrophic respiration) under Scots pine (green circle) and Pyrenean oak cover (red triangle). Data are mean values of plots with bars representing standard deviation ($n = 4$). SP: spring, SU: summer, AU: autumn and WI: winter. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

Fig. 3. Modelled response of soil CO₂ efflux (R_s : total soil respiration, R_H : heterotrophic respiration, R_A : autotrophic respiration) to the continuous interaction effect between soil temperature and soil water content (SWC) in Scots pine (a, c, e, respectively) and Pyrenean oak forests (b, d, f, respectively), according to the fitted models in Table 4.

transpiration (Poyatos et al., 2005), low growth rates (Camarero et al., 2010; Sabaté et al., 2002; Vayreda et al., 2012) and needle fall period from May to September (Díaz-Pinés et al., 2011a). The abundant precipitation in the first half of the year may delay the time at which drought stress becomes critical in the pine growing season. Soil temperature throughout winter and soil water availability throughout summer therefore constitute the main limitations for R_A in Scots pine,

closely linked to the main climate constraining factors for pine radial growth (Sánchez-Salguero et al., 2015).

The Pyrenean oak stand showed a distinct temporal evolution of R_A throughout the year, which we assume can be attributed to different leaf strategies influencing root phenological patterns (Curiel Yuste et al., 2004). Thus the lowest rates of R_A were registered during tree dormancy in winter. In early spring, with increasing soil temperatures

Fig. 4. Modelled daily rates of heterotrophic respiration (R_H) according to the parameterized models in Table 4; and estimated daily rates of autotrophic respiration (R_A) as the difference between modelled R_S and R_H in Scots pine (a) and Pyrenean oak forest (b). Lines represent mean values, and ribbons show the upper and lower 95% confidence intervals predicted by the models. SP: spring, SU: summer, AU: autumn and WI: winter.

Fig. 5. Relative contribution of soil heterotrophic respiration to total soil respiration under Scots pine and Pyrenean oak tree species. Lines represent daily means of predicted values for the study period (April 2014 to April 2017, $n = 3$ growing seasons). WI: winter, SP: spring, SU: summer and AU: autumn.

and optimum soil moisture conditions, we found a progressive rise in R_A when the oak became phenologically active (Salomón et al., 2016b). This rise in R_A peaked roughly three weeks before budburst (bud break occurs around DOY 145), probably fuelled by the mobilization of carbohydrate reserves in roots (Zhu et al., 2012) since there was no fresh assimilation of photosynthates or sap flow before leaf expansion (Salomón et al., 2016b). In June, R_A contributed up to ca. 30% to R_S , the highest proportion of the year. This is a time of high metabolic demand for leaf production (Lee et al., 2010) which lasts until photosynthetic activity is reactivated with leaf unfolding. Later in the summer, R_A rates decreased again across the drought period, which could be explained by the low fine root density and biomass attributed to the depletion of SWC in Mediterranean oak forests (López et al., 1998; Rey et al., 2002). The maximum contribution of R_A to R_S was again reached in mid-September, coinciding with the decreasing temperatures and the arrival of the autumn rainfall. We registered maintenance R_A rates when the oak entered dormancy during its litterfall period from October to December (Díaz-Pinés et al., 2011a).

Differences in R_A rates between species may not be completely attributable to plant phenology, since other plant traits and processes

may also be involved, such as transport patterns of root-respired CO_2 through the xylem, or different physiological strategies to deal with summer drought (Grossiord et al., 2012; Poyatos et al., 2005; Ubierna et al., 2009). We show strong evidence here that SWC and forest functional composition strongly influenced the temperature dependence of R_A and thereby R_S , providing important insights into the possible consequences of changes in forest composition. However, these major differences in R_S between oak and pine observed in our study site may have been particularly apparent due to the mild winters favouring Scots pine root activity and the intense summer drought causing evident R_A responses. The generalisation of our results should therefore be treated with caution.

4.3. Soil C stocks and cycling

Confirming our hypothesis, annual R_H was highest in the pine stand, where litterfall rates (Díaz-Pinés et al., 2011a) and C stored in the topsoil (Díaz-Pinés et al., 2011b) are significantly higher than in the oak stand. However, the C turnover rate in soils under pines was roughly twice that of oaks, reflecting the functional traits of leaves and needles

Table 5

Seasonal and annual total soil respiration (R_S) and its components (R_A : autotrophic, R_H : heterotrophic) estimated for each tree species (mean $\pm$ SD, $n = 3$) and given as $g\ CO_2\ C\ m^{-2}$. Turnover rate of soil C was calculated by considering the stored C in the forest floor plus 0–50 cm of mineral soil with stocks from Díaz-Piñés et al. (2011b). Different lowercase letters denote significant differences across seasons within the same tree species (linear models, $p < 0.05$). Capital letters denote significant differences between tree species within the same period.

Tree species	Soil CO ₂ efflux	Winter		Spring		Summer		Autumn		Annual		Turnover rate	
						(g m ⁻² season ⁻¹)				(g m ⁻² year ⁻¹)		(year ⁻¹)	
Scots pine	R _S	225 ± 25	A b	352 ± 26	a	229 ± 9.6	B b	247 ± 35	b	1.05 · 10 ³ ± 61			
	R _A	41 ± 2 (18%)	A ab	50 ± 8 (14%)	B a	7 ± 1.9 (3%)	B c	27 ± 11 (11%)	B b	124 ± 13 (12%)	B		
	R _H	184 ± 23 (82%)	b	302 ± 18 (86%)	A a	222 ± 7.8 (97%)	A b	220 ± 25 (89%)	b	929 ± 48 (88%)	A	0.10 ± 0.01	B
Pyrenean oak	R _S	167 ± 23	B	c313 ± 18	a	280 ± 2.3	A ab	243 ± 23	b	1.00 · 10 ³ ± 29			
	R _A	25 ± 8 (15%)	B c	84 ± 6 (27%)	A a	74 ± 3.0 (26%)	A ab	60 ± 5 (25%)	A b	243 ± 7 (24%)	A		
	R _H	142 ± 15 (85%)	c	229 ± 13 (73%)	B a	206 ± 0.9 (74%)	B ab	183 ± 19 (75%)	b	761 ± 22 (76%)	B	0.19 ± 0.01	A

–i.e. the nitrogen and lignin content of plant detritus in the litter layer (Gallardo and Merino, 1992; Melillo et al., 1982)– which is closely linked to tree C and its strategy for obtaining nutrients (Cornwell et al., 2008; Fernández-Alonso et al., 2018). This result contradicts the similarity in the potential decomposability of soil C between forest types that was found during an incubation experiment using mineral topsoil samples from the same study site (Díaz-Piñés et al., 2014). Some of the multiple factors affecting the apparent decomposability of soil C in the field and which may lead to differences in the results obtained under controlled conditions include changes in the composition and activity of the soil microbial community throughout the year, the presence of C pools of varying decomposability and physical protection, and the SWB. The lower decomposability of soil organic matter of pine origin may thus have contributed over centuries to the accumulation of greater soil C stocks than in the oak stand (Curiel Yuste et al., 2005). Our findings suggest that an upward shift by oak in the ecotone, induced by either climate change or forest management, will affect the soil's capacity to store C; however, the magnitude of the impact could be partly offset by a further intensification of soil microclimate constraints for R_H –i.e. higher temperatures and extended periods of drought, which may in turn slow the decomposition and release of soil C pools.

5. Conclusions

Our results clearly show different seasonal dynamics in soil metabolic activity between Pyrenean oak and Scots pine stands in a Mediterranean mountain area. Common patterns were also detected in the ecotone of both tree species, highlighting how the strong and inverse water and thermal seasonality of the Mediterranean climate constrains both microbial decomposition activity and root respiration. The consideration of the interaction effect between soil temperature and SWC was therefore critical for appropriately modelling the soil CO_2 efflux, and enabled us to detect a higher sensitivity of pine R_A than oak R_A to the summer drought period. The slow turnover rate of pine litter compared to oak-derived detritus may also have promoted soil C accumulation over the centuries. This greater understanding of the plant-soil system in the ecotone offers an insight into patterns that must be taken into account in future forest management. The forest's capacity to store soil C could be undermined by an oak expansion driven by current changing environmental conditions; however, the magnitude of the impact could be buffered by the further intensification of soil microclimate constraints on R_H .

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