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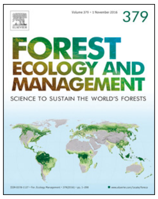

Disentangling the effects of tree species and microclimate on heterotrophic and autotrophic soil respiration in a Mediterranean ecotone forest

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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 conent (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

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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; ETo, 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

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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; Högberg 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 Rs (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_2O 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