



Drought-induced tree species replacement is reflected in the spatial variability of soil respiration in a mixed Mediterranean forest



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ABSTRACT

As episodes of drought-induced forest mortality are being increasingly reported worldwide and may become more frequent in the future as a result of climate change, it is essential to characterize their functional implications in terms of ecosystem carbon and water fluxes. We investigated the spatial variability of soil respiration in a mixed Mediterranean forest located on rugged terrain, where Scots pine (*Pinus sylvestris*) is affected by drought-induced dieback and appears to have been replaced by Holm oak (*Quercus ilex*) as the dominant tree species. Soil respiration was measured in spring 2010 on two plots (16.2 × 16.2 m) using a static closed chamber method (soda lime technique) and a systematic sampling (1.8-m grid) including 100 points per plot. Biotic and abiotic variables, such as soil moisture, soil temperature, soil organic matter content, stoniness, pH, fine root C:N ratio and biomass, tree basal area and tree species and health condition of nearest neighbouring tree were also recorded. Our results showed that the spatial variability of soil respiration under optimal environmental conditions (spring) was high and showed no spatial autocorrelation on the scale studied (1–18 m). A mixed-effects model applied to explain the spatial variability of soil respiration indicated that only the variables related to forest structure (i.e., health condition and basal area) explained any of the observed variability of soil respiration ($R^2 = 0.45$). Our model revealed that soil respiration was highest in soils close to dead pines and under Holm oak trees, suggesting that tree mortality and species replacement of pine trees by Holm oak may lead to higher soil respiration fluxes. The direct effect of tree mortality on soil respiration may be a transitory response caused by fine root mortality. Furthermore, the fact that tree species replacement as a result of drought-induced die-off is accompanied by concomitant changes in soil respiration has important implications for soil and ecosystem carbon balance.

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1. Introduction

Soil CO₂ fluxes, resulting from soil heterotrophic (microbes) and autotrophic (root and rhizosphere) respiration, are the second largest flux in the carbon balance of terrestrial ecosystems, after gross primary production (GPP) (Schlesinger and Andrews, 2000), and they play a crucial role in the global carbon cycle. However, given the large temporal and spatial variability of soil respiration, and our limited knowledge of the mechanisms underlying its variability (Curiel Yuste et al., 2007), it is still unclear how soil CO₂ efflux will respond to climate change. Understanding the factors controlling the large spatial variability in soil respiration will help improve future predictions of local-to-global C emissions.

One of the major questions that remain unanswered is the high spatial variability in soil respiration, from the scale of cm (Janssens and Ceulemans, 1998) to larger scales such as meso-scale/ecosystem (Søe and Buchmann, 2005; Rodeghiero and Cescatti, 2008) and macro-scales/regional (Janssens et al., 2001; Vargas et al., 2010). While climatic variables, e.g. soil temperature or soil moisture, determine most of the temporal variability in soil respiration at different scales (Pregitzer et al., 2000; Janssens et al., 2001; Davidson and Janssens, 2006), the spatial variability of soil respiration is determined by other factors, such as plant community composition, stand structure and/or soil organic matter content (Stoyan et al., 2000; Søe and Buchmann, 2005; Davi et al., 2006). The role of these variables also depends on the spatial scale under study. For instance, at the scale of cm (microscale) most of the variability in soil respiration is usually explained by soil moisture, litter biomass, fine root biomass and C:N ratio (Stoyan et al., 2000; Fóti et al., 2009; Martin and Bolstad, 2009), while at the scale of meters (mesoscale) plant proximity seems to play a very important

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role (Søe and Buchmann, 2005; Tang and Baldocchi, 2005). At the regional scale, ecosystem productivity coupled with temperature moisture interactions control soil respiration across ecosystems (Reichstein et al., 2003).

Most studies on the spatial variability in soil respiration in ecosystems have been conducted at the meso-scale level on flat terrains with relatively homogeneous conditions (Buchmann, 2000; Søe and Buchmann, 2005; Rodeghiero and Cescatti, 2008; Pickles et al., 2010). Much fewer studies have been carried out on rugged/heterogeneous terrains (Casals et al., 2000; Stoyan et al., 2000) which, even though these on the other hand, account for a substantial portion of the forested areas in the northern hemisphere, particularly in Mediterranean areas such as the Iberian Peninsula (Vallejo, 1983).

In addition to the complexity associated with rugged terrains, summer drought in the Mediterranean climate adds yet another level of complexity to our understanding of variability in soil respiration (Asensio et al., 2007a, b; De Dato et al., 2010; Cotrufo et al., 2011). Drought limits the physiological performance of both plants (Brunner et al., 2009; Nikolova et al., 2009) and microbes (Reichstein et al., 2002; Rey et al., 2002; Curiel Yuste et al., 2007), as well as the release of nutrients (Davidson and Janssens, 2006) and enzymes performance (e.g. Sardans and Peñuelas, 2005; Sardans et al., 2008) in the soil pore space. Moreover, the increased frequency and severity of drought events and heat waves (Carnicer et al., 2011) has been considered responsible for widespread events of drought-induced mortality (Allen et al., 2010), including several in the Mediterranean basin (Peñuelas et al., 2001; Martínez-Vilalta and Piñol, 2002; Bréda et al., 2006). This die-off is characterized by rapid defoliation and progressive increase in the mortality of over-storey trees (Bréda et al., 2006). Such widespread mortality may modify regional landscapes on a sub-decadal timescale, with significant implications for stand structure and dynamics and for ecosystem function (Royer et al., 2011). At the ecosystem scale, forest decline may trigger ecological succession and hence modify spatial patterns of plant distribution, which may also strongly affect soil respiration (Tedeschi et al., 2006; Wang and Epstein, 2012). An increase in the frequency, duration and severity of drought and heat stress associated with climate change could, therefore, influence spatial variation in soil respiration either directly (e.g. via limiting water for microbial/root respiration) or indirectly (e.g. via changing the composition, structure and distribution of forests) (Janssens et al., 2001).

We studied the spatial variability in soil respiration in a mixed forest of Scots pine (*Pinus sylvestris* L) and Holm oak (*Quercus ilex* L) in the Prades Mountains (NE Iberian Peninsula). Scots pine is one of the most widely distributed tree species on Earth (Critchfield and Little, 1966) and its southernmost and dry distribution limit lies on the Iberian Peninsula (Jalas and Suominen, 1976). In contrast, Holm oak, which is one of the most common Mediterranean tree species (Terradas, 1999), has its optimal distribution in the west of the Mediterranean Basin, including the Iberian Peninsula (Barbero and Loisel, 1992). The Scots pine population in Prades is affected by climatic drought-induced die-off (Martínez-Vilalta and Piñol, 2002; Hereş et al., 2011) and is seemingly being slowly replaced by the more-drought-adapted Holm oak (Vila-Cabrera et al., 2013).

In more detail, the specific objectives were: (1) To characterize the spatial variability (i.e. autocorrelation pattern) in soil respiration in a highly rugged mixed forest affected by drought-induced dieback. (2) To determine the minimum number of measurements necessary to estimate average soil respiration with a specific pre-defined precision. (3) To identify the role of biotic and abiotic factors determining spatial variability in soil respiration at the stand scale.

2. Materials and methods

2.1. Site description and experimental design

The study was carried out in a mixed forest in Titllar Valley, Prades Mountains (NE Iberian Peninsula; 41°13'N, 0°55'E), at an elevation of between 1010 and 1033 m a.s.l. The climate is typically Mediterranean with a mean temperature of 11.2 °C and annual mean rainfall of 720 mm (Climatic Digital Atlas of Catalonia (CDAC); (Ninyerola et al., 2000)). The substrate consists of fractured metamorphic schist that outcrops onto a large part of the study area. As a consequence of great stoniness combination with steepness (33° on average), the plots surface is very unstable, resulting in frequent movements surface mass. Additional information about the study area can be found in Hereter and Sánchez (1999).

The soils are xerochrepts with clay loam texture. However, they are only present in 56% of the study area, whereas the rest of the surface is directly covered by schist outcrops or stones that are just under the organic horizons. Organic horizons cover most of the soil surface with a variable thickness. The mixed forest is composed of Scots pine (*Pinus sylvestris* L) (54% of the total basal area [BA] and mean diameter at breast height [DBH] of 0.32 m) and the evergreen Holm oak (*Quercus ilex* L) (41% of the total BA and mean DBH of 0.15 m). The remaining woody vegetation includes *Quercus cerrioides* Willk. et Costa, *Taxus baccata* L, *Prunus mahaleb* L, *Ilex aquifolium* L, *Amelanchier ovalis* Medik., *Sorbus aria* L, *Sorbus torminalis* L and *Cistus laurifolius* L. The Scots pine population is affected by drought-induced die-off, with approximately 20% standing mortality and a varying degree of defoliation in surviving trees (Martínez-Vilalta and Piñol, 2002; Vila-Cabrera et al., 2013).

We aimed to survey a large number of sampling points, but it was not possible to measure more than 100 points per week. Thus, we measured soil respiration on different weeks and our experimental layout consisted of two plots (called A and B) of about 260 m² (16.2 × 16.2 m) separated by 65 m. Each plot had 100 measurement points on a regular grid (consecutive points separated by 1.8 m). Both plots were similar in slope and stand structure (Table 2). When, due to the great stoniness, it was impossible to take the soil measurements at the exact coordinates on the grid, the measurements were taken within a radius of 20 cm around the grid point, in suitable places. Despite this procedure, it was still impossible to obtain data from three points on plot A and two points on plot B. All the measurements were made in spring 2010 between April and May.

2.2. Soil respiration and soil parameters

Soil respiration was measured using the soda lime technique, which enabled us to take a large number of measurements simultaneously. Respiration was measured over two consecutive weeks in spring 2010, during the growing season, when temperature and moisture were not limiting factors. On each plot, soil respiration was measured twice at the sampling points in 24 h-cycles over two consecutive days. The two daily measurements were then averaged for each individual sampling point. In between the sampling weeks of the two plots, a storm of 75 mm occurred (Meteorological Service of Catalonia, www.meteocat.cat); this changed the environmental conditions and air temperature dropped by 11 °C.

To measure soil respiration we followed the protocol proposed by Keith and Wong (2006). We used soda lime in granules of 2–4 mm mesh size. Approximately 8 g of soda lime per dish (inert glass) from a total of 200 Petri dishes were oven-dried at 105 °C for 14 h. The dishes were then weighed in order to record the exact initial dry mass of soda lime. The soda lime was then remoisturized

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