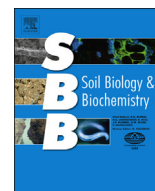




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Components, drivers and temporal dynamics of ecosystem respiration in a Mediterranean pine forest

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ABSTRACT

To investigate the climate impacts on the different components of ecosystem respiration, we combined soil efflux data from a tree-girdling experiment with eddy covariance CO₂ fluxes in a Mediterranean maritime pine (*Pinus pinaster*) forest in Central Italy. 73 trees were stem girdled to stop the flux of photosynthates from the canopy to the roots, and weekly soil respiration surveys were carried out for one year. Heterotrophic respiration (R_H) was estimated from the soil CO₂ flux measured in girdled plots, and rhizosphere respiration (R_{Ab}) was calculated as the difference between respiration from controls (R_S) and girdled plots (R_H).

Results show that the R_S dynamics were clearly driven by R_H (average R_H/R_S ratio 0.74). R_H predictably responded to environmental variables, being predominantly controlled by soil water availability during the hot and dry growing season (May–October) and by soil temperature during the wetter and colder months (November–March). High R_S and R_H peaks were recorded after rain pulses greater than 10 mm on dry soil, indicating that large soil carbon emissions were driven by the rapid microbial oxidation of labile carbon compounds. We also observed a time-lag of one week between water pulses and R_{Ab} peaks, which might be due to the delay in the translocation of recently assimilated photosynthates from the canopy to the root system. At the ecosystem scale, total autotrophic respiration (R_{At} , i.e. the sum of carbon respired by the rhizosphere and aboveground biomass) amounted to 60% of ecosystem respiration. R_{At} was predominantly controlled by photosynthesis, and showed high temperature sensitivity (Q_{10}) only during the wet periods. Despite the fact that the study coincided with an anomalous dry year and results might therefore not represent a general pattern, these data highlight the complex climatic control of the respiratory processes responsible for ecosystem CO₂ emissions.

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1. Introduction

The amount of carbon released by ecosystem respiration represents the second largest CO₂ flux after photosynthesis (IPCC, 2013). In order to predict likely changes of the terrestrial carbon

balance under varying environmental conditions, it is fundamental to quantify the different sources of the ecosystem CO₂ efflux and their dependence on biotic and environmental drivers. The total flux of CO₂ released from the ecosystem (R_{eco}) can be partitioned into soil respiration (R_S) and aboveground autotrophic respiration (R_{Aa}). R_S can be further partitioned into that originating from roots and closely associated microorganisms, such as mycorrhizas (i.e. belowground autotrophic or rhizosphere respiration, R_{Ab}) and the flux produced from the decomposition of dead organic matter (i.e. microbial or heterotrophic respiration, R_H) (Eq. (1), Hanson et al., 2000; Kuzyakov, 2006; Heinemeyer et al., 2007):

$$R_{eco} = R_S + R_{Aa}, R_S = R_{Ab} + R_H \quad (1)$$

Abbreviations: GPP, gross primary productivity; NEE, net ecosystem exchange; R_{eco} , ecosystem respiration; R_{Ab} , belowground autotrophic respiration; R_{Aa} , aboveground autotrophic respiration; R_{At} , total autotrophic respiration; R_H , heterotrophic respiration; R_S , soil respiration ($R_S = R_H + R_{Ab}$); SWC, Soil water content.

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The monitoring of the total soil CO₂ efflux can be performed with robust and consolidated methods, such as static or dynamic chamber systems equipped with infrared gas analysers (Davidson et al., 2002). However, the partitioning of R_{eco} and R_{S} into individual sources remains a challenging task, for which several techniques have been developed and tested over the past few decades. Most of these methods cannot be applied to forests since they are often impractical and/or limited in their spatial and temporal analysis of the phenomena (for a review, see Hanson et al. (2000) and Kuzyakov (2006)).

In the past decade, the tree girdling approach has been successfully applied to forest ecosystems (Hogberg et al., 2001; Bhupinderpal-Singh et al., 2003; Subke et al., 2011). The method is based on the removal of the bark and outer vascular tissues (phloem) to stop the flow of photosynthates to the roots, which causes a rapid and strong suppression of root and rhizomicrobial respiration (Hogberg et al., 2001). Soil respiration measurements performed on girdled plots after an initial settling-down period can be used to directly derive R_{H} (Hogberg et al., 2001). Tree-girdling can lead to an overestimation of the proportion of R_{H} due to roots' residual respiration and decomposition (Bhupinderpal-Singh et al., 2003). However, compared to other partition techniques (i.e. root trenching), girdling has the advantage of preserving the soil–root structural integrity and the xylematic water transport, so that soil moisture and temperature are generally unaltered for several months after the treatment (Kuzyakov, 2006; Ekberg et al., 2007).

Published results of tree girdling experiments report that the R_{Ab} contribution to R_{S} ranges from 24 to 65% in forest soils across different biomes and ecosystem types (Hogberg et al., 2001; Bhupinderpal-Singh et al., 2003; Andersen et al., 2005; Olsson et al., 2005; Binkley et al., 2006; Frey et al., 2006; Scott-Denton et al., 2006; Johnsen et al., 2007; Högberg et al., 2009; Chen et al., 2010; Subke et al., 2011; Levy-Varon et al., 2012; Bloemen et al., 2014). However, most of these girdling experiments have been performed in boreal, temperate or subtropical forests, and there is a general lack of information on water-limited environments such as Mediterranean ecosystems.

Mediterranean forests and shrublands cover an area of about 2.75 million km² (Rambal, 2001), and are characterised by high inter-annual climate variability (Luterbacher et al., 2006). Several studies highlight the fact that soil and ecosystem carbon fluxes in these ecosystems are strongly affected by the erratic seasonal and inter-annual distribution of rain events (Valentini et al., 2000; Almagro et al., 2009; Jongen et al., 2011; Ross et al., 2012; Poulter et al., 2014). While R_{S} is generally constrained by low soil water content during summer months, abrupt and large soil CO₂ pulses have been observed after rewetting the dry soil (Birch, 1958; Jarvis et al., 2007; Inglima et al., 2009; Unger et al., 2012; Matteucci et al., 2014). These intense emissions can substantially affect the annual carbon balance and highlight the vulnerability of soil carbon stocks in these ecosystems (Borken and Matzner, 2009; Moyano et al., 2013). The Mediterranean climate is expected to be affected by a reduction in the intensity and distribution of rainfall (Trenberth et al., 2003; Tebaldi et al., 2006; Christensen et al., 2007; Trenberth, 2011; IPCC, 2013). The prediction of the impacts of these climate changes on soil carbon dynamics requires new insights into and observations of the processes and drivers that affect the different components of respiration.

For this purpose we present the results of a tree girdling experiment carried out in a Mediterranean maritime pine forest (*Pinus pinaster*) in Central Italy, which is equipped with an eddy covariance micrometeorological tower. Ecosystem fluxes were analysed together with soil CO₂ fluxes throughout the first year following the girdling treatment. The novel combination of these

two methodologies allowed us to quantify all the different components of ecosystem respiration and to: (1) partition soil fluxes into their autotrophic and heterotrophic components; (2) partition total autotrophic respiration (R_{At}) into above- and belowground sources; (3) follow the seasonal evolution of the partitioned components; (4) analyse in detail the environmental and biological drivers that affect the response of the different components of R_{eco} . The study period coincided with a severe drought interspersed with sporadic rain events. Particular attention was given to the temporal response of R_{S} to sudden rain pulses.

2. Materials and methods

2.1. Site description

The study site is located in a maritime pine forest in Central Italy (Tuscany). The experimental area lies within the boundaries of the Regional Park of San Rossore–Migliarino–Massaciuccoli (43°43'43" N, 10°17' 13" E, 6 m a.s.l.), in an almost flat area (slope < 3%) characterised by the presence of sandy dunes and located between the Arno and Serchio rivers, 800 m inland from the sea coast.

The area is characterised by a typical Mediterranean climate, with humid and mild winters and dry and hot summers. The long-term (1980–2012) mean annual air temperature is 15.35 °C, with the highest value measured in August (24.16 °C) and the lowest in January (7.4 °C). Mean annual precipitation (1980–2012) amounts to 883 mm, 50% of this being concentrated in the autumn months. The driest month is July with a mean rainfall of 18 mm, while October and November are the wettest, with 138 mm each. Long-term climate data were obtained from a meteorological station (Regional Hydrologic Service of Tuscany) located 10 km from the study site. Meteorological data have been collected at the flux tower since the year 2000. The wind regime is characterised by a sea–land breeze circulation, i.e. the air flows quite predictably from the West (sea) during the day and from the East (land) during the night (Fig. 1, inset).

The dominant species is *P. pinaster* Ait., with sparse *Pinus pinea* L. and *Quercus ilex* L. trees. The average stem density is 565 trees ha⁻¹, the average diameter at breast height is 29 cm, and the average canopy height is 18 m. Ground vegetation is represented by sparse *Erica arborea*, *Phyllirea angustifolia*, *Rhamnus alaternus* and *Myrtus communis*. The vegetation was naturally renovated following a wildfire in 1944 and therefore, at the moment of this study, was 67 years old. Root biomass is concentrated at between 0 and 40 cm. Total root biomass in the first 25 cm of the soil profile is 2.2 kg fresh weight m⁻², and the root/shoot ratio is 0.18. The water table depth ranged from 69 cm in April 2011 to 174 cm in November 2011, and can be reached by the taproot of maritime pine (Zenone et al., 2008).

The soil is a sandy calcareous regosol with a content of 93% sand, 4% clay and 3% silt in the first 10 cm of the soil profile. The organic layer has a thickness of 2.7 ± 0.4 cm, 43.8% soil organic carbon content, a C/N ratio of 32.5 and a pH of 4.4. The carbon content and C/N ratio are, respectively, 13.9% and 30 in the uppermost 1 cm of mineral soil, 1% and 13.5 in 10-cm deep mineral soil. The annual N deposition is about 12 kg N ha⁻¹ (Rosenkranz et al., 2006).

2.2. Soil respiration measurements

In March 2011, six circular plots (20-m diameter) were delimited at the long-term eddy covariance experimental site of San Rossore. In order to minimise the impact of the girdling experiment (see below) on eddy covariance measurements, plots were located at

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