



Research paper

Effect of environmental variables and stand structure on ecosystem respiration components in a Mediterranean beech forest

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The temporal variability of ecosystem respiration (R_{ECO}) has been reported to have important effects on the temporal variability of net ecosystem exchange, the net amount of carbon exchanged between an ecosystem and the atmosphere. However, our understanding of ecosystem respiration is rather limited compared with photosynthesis or gross primary productivity, particularly in Mediterranean montane ecosystems. In order to investigate how environmental variables and forest structure (tree classes) affect different respiration components and R_{ECO} in a Mediterranean beech forest, we measured soil, stem and leaf CO_2 efflux rates with dynamic chambers and R_{ECO} by the eddy-covariance technique over 1 year (2007–2008). Ecosystem respiration showed marked seasonal variation, with the highest rates in spring and autumn and the lowest in summer. We found that the soil respiration (SR) was mainly controlled by soil water content below a threshold value of $0.2 \text{ m}^3 \text{ m}^{-3}$, above which the soil temperature explained temporal variation in SR. Stem CO_2 effluxes were influenced by air temperature and difference between tree classes with higher rates measured in dominant trees than in co-dominant ones. Leaf respiration (LR) varied significantly between the two canopy layers considered. Non-structural carbohydrates were a very good predictor of LR variability. We used these measurements to scale up respiration components to ecosystem respiration for the whole canopy and obtained cumulative amounts of carbon losses over the year. Based on the up-scaled chamber measurements, the relative contributions of soil, stem and leaves to the total annual CO_2 efflux were: 56, 8 and 36%, respectively. These results confirm that SR is the main contributor of ecosystem respiration and provided an insight on the driving factors of respiration in Mediterranean montane beech forests.

Keywords: ecosystem respiration, *Fagus sylvatica*, leaf respiration, soil CO_2 efflux, stem CO_2 efflux, total non-structural carbohydrates.

Introduction

Forest ecosystems play a crucial role in the global carbon cycle, accounting for most of terrestrial primary productivity (Geider et al. 2001, Beer et al. 2010). The amount of CO_2 that

is absorbed or emitted by a forest ecosystem is defined as net ecosystem exchange (NEE) and it is the difference between two large ecosystem fluxes of similar magnitude: gross primary productivity (GPP) and ecosystem respiration (R_{ECO}) (Schulze et al. 2000). Ecosystem respiration constitutes between 70

and 85% of annual GPP (Luyssaert et al. 2007, 2009) and is often the main determinant of the observed NEE variability (Valentini et al. 2000, Janssens et al. 2001, Griffis et al. 2004), particularly in broad-leaved forests (Stoy et al. 2008). NEE of different ecosystems is being measured across the world within the international network FLUXNET (<http://fluxnet.ornl.gov>) using the eddy-covariance technique (Baldocchi et al. 2001). It is a widely used technique, based on the covariance between turbulent fluctuations of the vertical wind speed and CO₂ concentration that allow us to estimate the carbon, water and energy exchanges between an ecosystem and the atmosphere without any perturbation over relatively large terrains (Foken et al. 2012).

Although the eddy-covariance technique allows an estimation of R_{ECO} (Reichstein et al. 2012) after applying different partitioning techniques (Reichstein et al. 2005, Lasslop et al. 2010), only chamber methods can estimate the contribution of the main different components of R_{ECO} : soil respiration (SR), stem CO₂ effluxes (SCE) and leaf respiration (LR). At a global scale, SR accounts for 98 Pg year⁻¹, the second largest flux between the terrestrial biosphere and the atmosphere (Bond-Lamberty and Thomson 2010) and an order of magnitude larger than fossil fuel emissions (Denman et al. 2007). SR contributes ~30–80% of R_{ECO} (Janssens et al. 2001, Davidson and Janssens 2006), while the remaining CO₂ losses are from woody, foliar tissues (Lavigne and Ryan 1997, Bolstad et al. 2004, Curtis et al. 2005, Tang et al. 2008) and to a small extent from coarse woody debris (Gough et al. 2007). In order to predict how NEE and R_{ECO} will respond to climate change it is necessary to understand how different respiration components will be affected by environmental variables. Among the environmental factors that control ecosystem respiration and its components, temperature plays a fundamental role affecting soil (Lloyd and Taylor 1994), stem (Edwards and Hanson 1996), leaf (Tjoelker et al. 2001) and thus ecosystem respiration (Mahecha et al. 2010). In Mediterranean regions, the seasonal drought occurring in summer periods often limits SR (Rey et al. 2002, 2005, 2011, Reichstein et al. 2003, de Dato et al. 2010) as well as other respiration components (Reichstein et al. 2002, Ciais et al. 2005, Saveyn et al. 2007) and thus, soil moisture also plays a crucial role limiting CO₂ effluxes in many ecosystems. Although the importance of R_{ECO} has been widely recognized, there are few studies focusing on the response of different R_{ECO} components to environmental variables (Law et al. 1999).

Beside environmental variables, stand structure also plays an important role in determining LR and SCE: LR rates can vary throughout the canopy (Bolstad et al. 1999, Griffin et al. 2001) together with photosynthetic capacity (Field 1991, Hollinger 1996, Calfapietra et al. 2005), soluble sugars and starch concentrations, which are the respiratory substrates (Azcon-Bieto and Osmond 1983, Griffin et al. 2002), and foliar nitrogen

concentration, which has been shown to decrease from the top to the bottom of the canopy (Ellsworth and Reich 1993, Hollinger 1996, Griffin et al. 2001, Gielen et al. 2003) and to be positively correlated with LR rates (Reich et al. 2006, Gonz  les-Meler et al. 2009). Similarly, although the SCE is subjected to spatial variation as a result of different wood composition, growth rates and living cells distribution (Stockfors 2000, Ceschia et al. 2002), little or no information is available on the effect of the stand structure, particularly tree social status (i.e., dominant, co-dominant trees).

A better understanding of how these factors control R_{ECO} and its components is essential for a reliable prediction of the impact of climate change on ecosystem functioning. Furthermore, state and function parameters are required to improve current models on plant and ecosystem carbon balance to better predict possible feedback between forest ecosystems and climate. In this study, we used measurements of SR, SCE and LR by dynamic chamber and R_{ECO} estimates by the eddy-covariance technique to analyze environmental and structural drivers of R_{ECO} in a Mediterranean montane beech forest. The specific hypotheses we tested were: (i) could the low summer water content characteristic of the Mediterranean region limit R_{ECO} , even in a montane area? (ii) Do the ecosystem components respond differently to the environmental variables, explaining the seasonal variation of R_{ECO} ? (iii) Do respiration rates vary according to tree social position and canopy layers?

Materials and methods

Site description

The experimental site is located in Selva Piana, a beech (*Fagus sylvatica* L.) forest in Collelongo (AQ, central Italy; coordinates 41°50′58″N—13°35′17″E, 1560 m above sea level). The climate is Mediterranean montane, with a mean annual temperature of 7.1 °C and mean temperatures of the coldest and warmest months are −1.1 and 16.4 °C, respectively. Mean annual precipitation is 1104 mm, of which between 1996 and 2007 ~10% falls in summer. The stand vertical structure is composed of two layers: a dominant and a co-dominant one (Masci 1995). Stand density is 825 trees ha⁻¹, the mean age in 2008 was 115 years, basal area was 40.6 m² ha⁻¹ with a mean diameter of 25 cm and a mean height of 21.2 m. Soil depth exhibits high spatial variability ranging from 40 to 100 cm and is classified, according to the IUSS working group WBR (2006) as a Humic Alisol (Chiti et al. 2010). The site is equipped with an eddy-covariance tower measuring the exchange of CO₂, H₂O and energy fluxes since 1993 (Valentini et al. 1996) and is part of the CARBOEUROPE, FLUXNET and ILTER international networks.

Soil CO₂ efflux

In April 2007, 10 experimental plots (5 × 5 m) were randomly established within the ‘footprint’ of the eddy flux tower. In each

plot, five soil collars were gently inserted into the soil according to a circular distribution spaced a minimum of 50 cm away from the neighbouring trees. The collars were made of PVC tubes (10 cm diameter and 5 cm high, a total of 50 points) with two stainless steel legs to facilitate the insertion into the ground leaving 2 cm above the soil surface. Soil CO₂ effluxes were measured with a closed dynamic system (EGM 4, PP-System, Hitchin, UK), connected to an SRC-1 Soil Respiration Chamber (PP-System, Hitchin, UK). The system measures the change in CO₂ concentration inside the chamber within a 90–120 s interval; the CO₂ concentration increase range was generally between 10 and 50 ppm. Soil CO₂ efflux was measured every 2–6 weeks from May 2007 until May 2008 for a total of 11 measurement campaigns, except for the period between December to March when snow covered the soil. During the SR measurements, soil temperature at 5 cm depth (T_s) was measured with a soil temperature probe STP-1 (PP-System, Hitchin, UK) and soil water content between 0–10 cm depth (SWC) by time domain reflectometry technique (Trime-FM, IMKO, gmbH, Ettlingen, Germany).

Stem CO₂ efflux

Stem CO₂ effluxes were measured on 10 trees over the growing season of 2007 and over a winter campaign in February 2008; air temperatures (T_{air}) were similarly recorded. Tree selection was stratified according to the stand vertical structure: five trees in the dominant class (tree height >20 m) and five in the co-dominant class (tree height <20 m). In the Collelongo experimental site, this threshold corresponded to the classification proposed by Bechtold (2003) based on canopy position and light exposure: the dominant trees had crowns extending above the general level of the crown canopy and received full light from above and partly from the sides, while the co-dominant trees had crowns at the general level of the crown canopy and received full light from above but little direct sunlight penetrates from the side.

Gas exchange rates were measured by a modified-Plexiglas cuvette (PLC-2, Analytical Development Company, Hoddeson, UK), with a volume of 108 cm³ and covered stem area of 36 cm². The cuvette was equipped with a neoprene gasket, positioned over a mosses-free stem surface at 1.30 m height and sealed by Terostat (Henkel KgaA, Germany). A black cloth was used to cover the cuvette at the time of the measurement to avoid CO₂ refixation by the beech photosynthetic bark (Berveiller et al. 2007). The cuvette was connected to the LCA-4 open-system infrared gas analyzer (Analytical Development Company, Hoddeson, UK) and left in position for 10 min to stabilize. Air temperature was measured by a thermocouple positioned inside the chamber. The measurements were performed at breast height (1.3 m), because it provides an acceptable estimation of respiration of the whole stem (Stockfors 2000).

Leaf respiration and leaf biochemical measurements

Leaf respiration, total non-structural carbohydrates (TNC) measured as the sum of soluble sugars and starch content, leaf mass per area (LMA) and carbon to nitrogen ratio (C/N) were measured in fully expanded leaves on one occasion in July 2007. Some technical problems prevented repetition over the growing season. These measurements were carried out on 10 leaves from the sun and shade canopy layers (25 and 17 m, respectively). The leaves were collected at three different periods of the day including pre-dawn and noon. The leaves were detached with the petiole, placed in water and darkened for 15 min prior to measurements. This did not alter LR rates, as confirmed by preliminary tests. Leaf respiration was measured using a portable gas exchange system (LiCor 6400, Lincoln, NE, USA) at a constant leaf temperature set at 15 °C. These leaves were also used for leaf biochemical determinations. Three subsample leaf discs (8 mm diameter) were taken on six leaves, three per layer, and immediately frozen in liquid nitrogen. Total non-structural carbohydrates were extracted according to Luo et al. (2006) and their concentration was determined measuring the radiation absorbance at 340 nm (Perkin-Elmer UV/VIS Spectrophotometer Lambda 3B, Waltham, MA, USA).

Leaf area was determined on the remaining four leaves (two per layer) with an image analyzer (SKYE Instruments Ltd, Powys, UK). Then, the leaves were dried in a ventilated oven at 70 °C for 2 days, weighed and powdered in a mortar and pestle cooled with liquid nitrogen. The C/N ratio was determined by a CHN-elemental analyzer (Carlo Erba Strumentazione, Milan, Italy). The LMA, determined as the ratio of the dry mass over the leaf fresh area, allowed us to calculate the TNC concentration and LR per unit of leaf mass.

Ecosystem respiration

Ecosystem CO₂ fluxes have been measured at the site since 1993 using the eddy-covariance technique (Valentini et al. 1996) and afterwards following the FLUXNET methodology (Aubinet et al. 1999). The experimental set-up consisted of a fast-response infrared gas analyzer (LI-7000, LI-COR, Lincoln, NE, USA) and a three-dimensional sonic anemometer (CSAT3, Campbell Scientific, Logan, UT, USA). Air was drawn through the analyzer by a pump (VDO M48 × 25/l, Antriebstechnik GmbH, Germany) installed downstream of the analyzer. Measurements were stored as half hour means in a data logger (CR1000, Campbell Scientific).

Ecosystem respiration (R_{eco-ec}) was calculated as the sum of night-time fluxes (integrated with the storage flux and corrected for the underestimation of flux under low turbulence conditions) and day-time respiration (extrapolated by temperature functions) or the whole-day CO₂ fluxes for the non-vegetative period. All the corrections and the gap-filling techniques were performed with standard FLUXNET procedures (Papale and Valentini 2003, Papale et al. 2006).

Scaling-up CO₂ efflux to daily and stand-level bases

To scale up the spot SR measurements to daily and annual bases, we fitted different equations to describe the dependencies of SR to solely T_s (Eq. 1) or solely soil water content (Eq. 2). Considering the strong correlation between T_s and SWC at seasonal scale (data not shown), we used separate regressions to describe the dependence of SR on both variables. Measurements taken at soil temperature $<10^\circ\text{C}$ were representative of the unwaterstressed period, whereas SR measurements made at T_s values $>10^\circ\text{C}$ were chosen as representative of the waterstressed period.

For the unwaterstressed period, the equation was:

$$\text{SR} = \text{SR}_{10} Q_{10}^{(T_s - 10/10)} \quad (1)$$

where SR_{10} (SR at 10°C), Q_{10} (temperature sensitivity of SR) are the estimated parameters and T_s is the measured soil temperature ($^\circ\text{C}$) at 5 cm depth.

SR measurements made when soil temperature was $>10^\circ\text{C}$ were used to fit the dependence of SR on soil water content as follows:

$$\text{SR} = a\text{SWC}^2 + b\text{SWC} + c \quad (2)$$

where SWC is the soil water content measured at 0–10 cm depth; a , b and c are the estimated parameters.

The use of models where T_s and SWC was combined to describe SR suffered from an uneven distribution of residuals (data not shown), thus the annual estimate of SR was obtained by integrating the fluxes calculated using Eq. (1) or (2), applied in relation to T_s measured continuously at the site.

The dependence of SCE was described separately for the two different tree classes as follows:

$$\text{E} = \text{SCE}_{15} Q_{10}^{(T_{\text{air}} - 10/10)} \quad (3)$$

where SCE_{15} (SCE at 15°C) and Q_{10} (temperature sensitivity of SCE) are the estimated parameters and T_{air} is the measured air temperature ($^\circ\text{C}$). The SCE expressed per unit of soil surface (SCEs, $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$) was calculated as the product of SCE and the woody surface area per unit of forest soil (WSA, m^2 stem surface per m^2 of ground). The WSA was estimated by combining a site-specific allometric relationship between diameter at breast height (1.3 m) and woody (stem and branches) surface area (Matteucci 1998) with the stem distribution (number of stems per hectare, 5 cm size-class) and the stand hypsometric relationship (tree height–tree diameter). The annual estimate of SCEs was obtained by integrating the fluxes using the Eq. (3), according to T_{air} .

Leaf respiration measured at the constant temperature of 15°C did not allow us to estimate the temperature sensitivity of LR. For the time-integration of LR, the temperature dependency

of LR was described using a Q_{10} function using air temperature according to the equation developed by Tjoelker et al. (2001):

$$0 = 3.22 - 0.046T_{\text{air}} \quad (4)$$

where Q_{10} is the temperature sensitivity (see explanation before) of LR and T_{air} is air temperature. The integration at canopy level was obtained by using the leaf area index (LAI) estimated by MOD15A2 that gives an 8-day-composite LAI ($\text{m}^2 \text{ m}^{-2}$) with a 1 km resolution (Oak Ridge National Laboratory Distributed Active Archive Center [ORNL DAAC]). A smoothed function based on the MOD15A2 data was used to interpolate the LAI on a daily scale. The partition of the LAI into sun and shaded leaves was based on a precedent study carried out at the same site (Matteucci 1998).

Soil temperature, SWC and T_{air} measured at the same time of the gas exchange measurements were used to calibrate the continuous half hour measurements of the meteorological tower used for daily integration.

Statistical analysis

Repeated-measures ANOVA was used to test the seasonal variations in SR and to test the tree social class effect on SCE, with the diameter at breast height as covariate and Fisher's post hoc test. Overall differences were considered significant with a P value of <0.05 . Overall differences between sun and shade leaves in LR, and leaf characteristics were calculated using Student's t -test. The differences were considered significant at $P < 0.05$. Statistical analysis required us to obtain the regression coefficients performed by SYSTAT 11 (SPSS Inc., Chicago, IL, USA).

Results and discussion

Soil CO₂ effluxes

Seasonal changes in SWC regulated the response of SR to temperature. This is not surprising, as soil temperature and soil water content were negatively correlated as often occurs in Mediterranean climates (e.g., Rey et al. 2002). T_s peaked in summer when SWC was at its minimum, and the minimum T_s was recorded in winter when the SWC reached its maximum (Figure 1). During spring, characterized by mild soil temperature and high soil water content, SR increased slightly until a maximum rate of $2.64 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ was recorded at the beginning of June. Afterwards, following a decrease in SWC, SR started to decline, reaching the minimum rate of $0.77 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ in August 2007. After the autumn rains, occurring at the beginning of October 2007 when the temperature was still high, a second peak of SR was measured ($2.53 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$). In winter, although SWC was at its maximum, low soil temperatures limited SR. In spring 2008, the SR increased steadily after snow melting. The range of soil CO₂

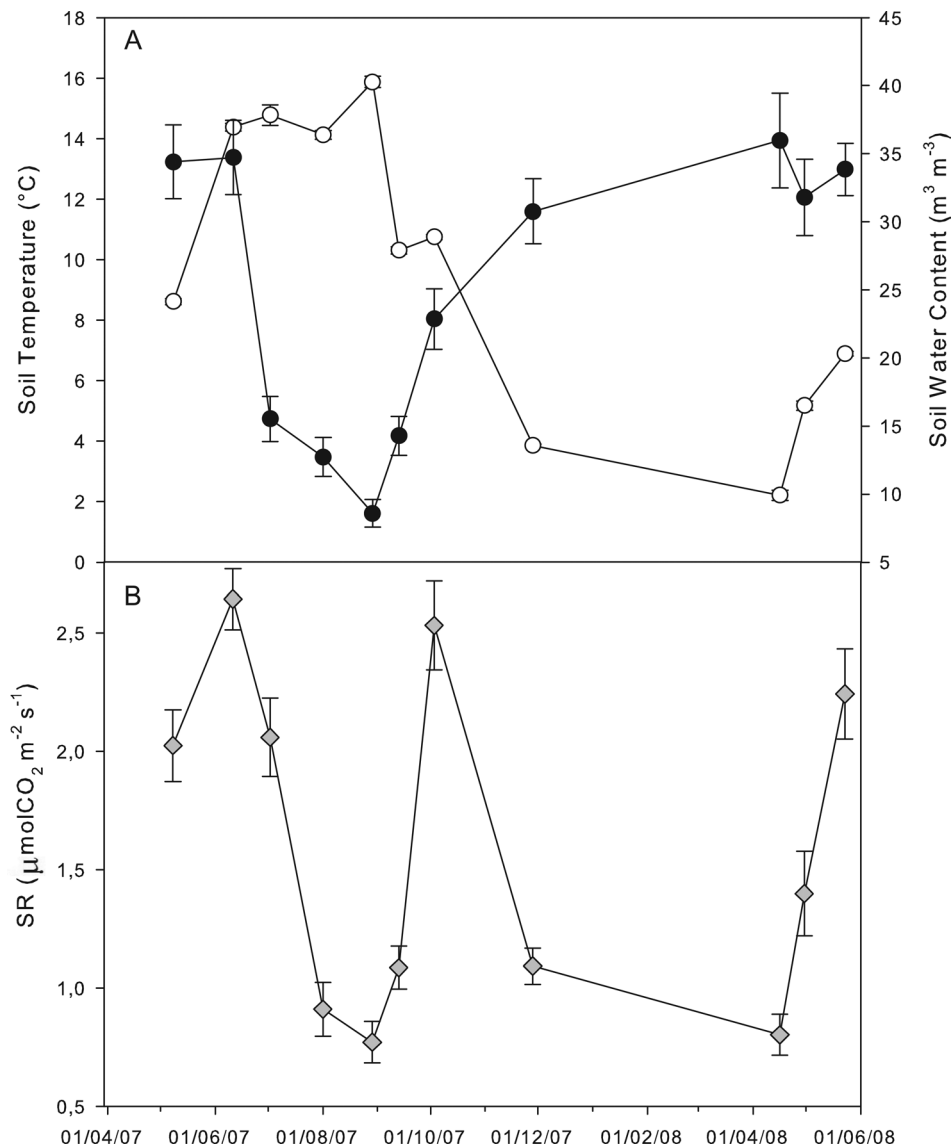


Figure 1. Temporal course of soil temperature (white circles), soil water content (black circles) and soil CO₂ efflux (SR) (grey diamonds) during 2007–2008. Vertical bars indicate standard errors of the mean ($n = 10$).

efflux rates measured in this study is consistent with those found in a previous study at the same site (Matteucci et al. 2000) and in other beech forests in Europe (Epron et al. 1999, Janssens and Pilegaard 2003).

Soil CO₂ efflux was related to T_s according to an exponential relationship (Figure 2A) when T_s was lower than 10 °C (spring, autumn and winter). In spring, coinciding with the start of the tree growing season, the increase in the population of respiring microorganisms together with increased fine root growth may have confounded the response of SR to climate, as has often been observed (Baldocchi et al. 2006). The estimated SR at 0 °C was 0.69 and the derived Q_{10} was 3.36. This 'apparent' Q_{10} value (Davidson and Janssens 2006) estimated during the unwaterstressed period was within the range of Q_{10} values (3.3 ± 1.1) reported in a recent global SR database (Bond-

Lamberty and Thomson 2010). On the other hand, the SR rates measured in periods when soil temperature values were >10 °C were strongly correlated with SWC (Figure 2B). The effect of SWC on SR showed a threshold value of 0.2 m³ m⁻³, below which the SWC solely controlled temporal variability in SR. The same threshold value was reported for a coppice oak forest in Central Italy (Rey et al. 2002).

The observed strong reduction of SR during summer is comparable to those reported for other Mediterranean ecosystems (Reichstein et al. 2002, Rey et al. 2005, 2011, de Dato et al. 2010, Misson et al. 2010) despite our site being a montane subtype. At our site, the first severe reduction in SWC occurred in July, but it was not coupled to the same extent by an SR reduction, which occurred only later with a further reduction of SWC (Figure 1). The first, more limited, reduction could be the

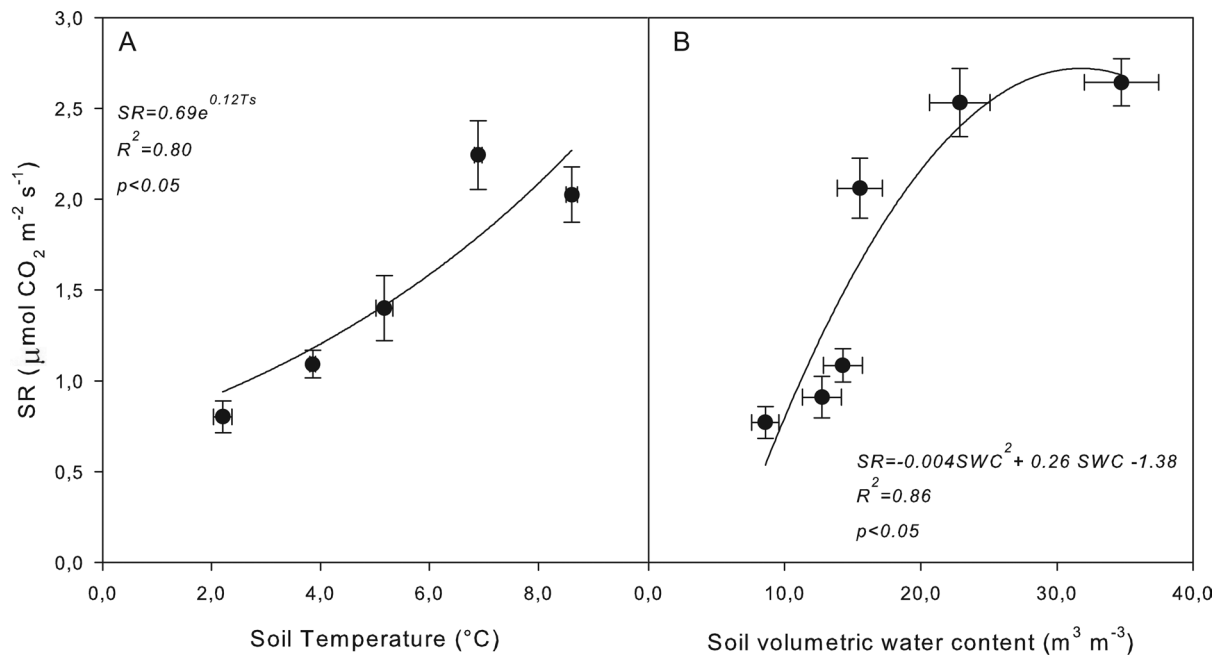


Figure 2. Relationship between soil CO₂ effluxes (SR) and soil temperature for $T_s < 10$ °C (A) and between SR and SWC for days with $T_s > 10$ °C (B). Circles are mean of measurements performed on the same date ($n = 10$).

result of inhibition of microbial activity, whereas the second, larger, reduction could be caused by a decrease of root respiration that may contribute to a delayed response of SR to summer drought (Davidson et al. 1998). This delay could be relatively long in beech trees with a deep-reaching root system that has high capacity of water uptake (Schmid and Kazda 2002). In addition to the seasonal changes of T_s and SWC, root phenology and substrates' quality/quantity changes may have affected SR (Kuziyakov and Gavrichkova 2010, Ruehr and Buchmann 2010). In our site, the spring peaks could be partly related to root growth (Scarascia-Mugnozza et al. 2000), while the autumn one to the fine root mortality (Monaco et al. 1993) and/or to the input of 'fresh' aboveground litter over the soil.

The estimated amount of carbon released via the SR over the year was ~ 430 g C m⁻² year⁻¹, which is in the range reported for forests: Raich and Schlesinger (1992) for broadleaved forests (300–1414 g C m⁻² year⁻¹), Janssens et al. (2001) for 19 European forests (660 ± 290 g C m⁻² year⁻¹) and Granier et al. (2003) for several European beech forests (between 377 and 887 g C m⁻² year⁻¹). Higher values (898 g C m⁻² year⁻¹) of carbon lost through SR have also been reported by Knohl et al. (2008) for an old beech forest and by Matteucci et al. (2000) for the same site of this study but during a different year (1996). Excluding structural changes of the forest between the two study years (Matteucci et al. 2007), the lower values of the year 2007 could be explained by the strong drought that occurred in this year compared with 1996. Indeed, between July and August 1996, rainfall amounted to 35 mm, whereas only 3 mm were recorded for the same months in 2007.

Stem CO₂ effluxes

Stem CO₂ effluxes showed a similar seasonal trend in both dominant and co-dominant trees (Figure 3B), even if the amplitude of the summer peak (August) was lower in co-dominant trees (0.54 μmol CO₂ m⁻² s⁻¹) compared with the dominant ones (1.47 μmol CO₂ m⁻² s⁻¹). In contrast, during winter, there were no significant differences in SCE between co-dominant and dominant trees (February 2008; 0.05 μmol CO₂ m⁻² s⁻¹ as mean value). These results agree with the findings of a previous study carried out at the same experimental site (Matteucci et al. 1999), and are in the range reported for temperate forest trees in China (Wang et al. 2010) but lower than those reported for a current year beech stem (Berveiller et al. 2007). In our study, the SCE rates measured in the dominant trees were systematically larger than those measured in the co-dominant class (Figure 3B), whereas T_{air} was the same for both tree categories (Figure 3A). Beyond the well-known diameter effect on beech SCE (Valentini et al. 1996, Damesin et al. 2002), these results suggest that, although beech is a shade-tolerant species, the dominant trees seem to have access to a quantitatively and qualitatively different light (De Angelis and De Luca 1998). This could favour growth (Falster and Westoby 2003) and, in turn, increase carbon allocation to stem tissue and growth (Lavigne and Ryan 1997, Damesin et al. 2002, Gruber et al. 2009) in dominant trees.

This hypothesis is corroborated by the measurements carried out during the dormant season, where the SCE rates between the two social classes did not show any significant differences (Figure 3B).

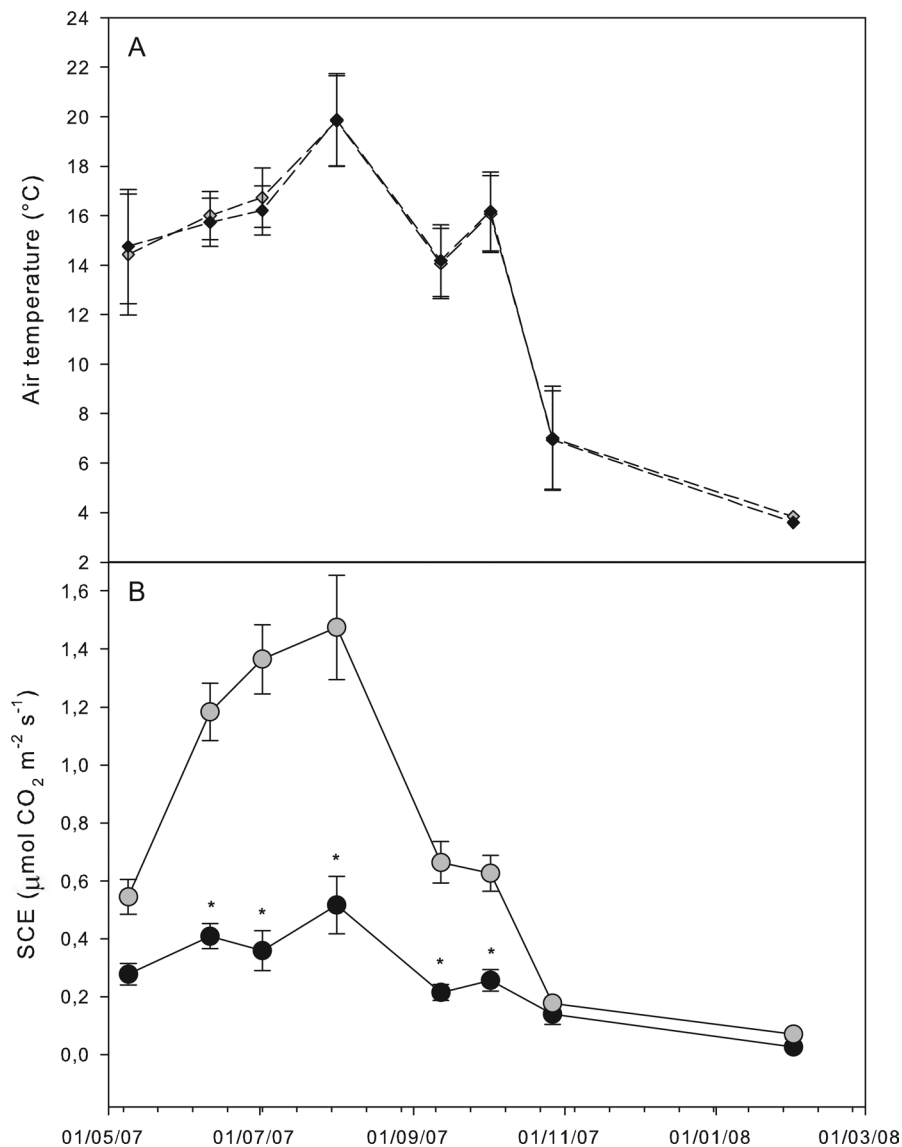


Figure 3. (A) Temporal course of air temperature (°C) of dominant and co-dominant stems (grey and black diamonds, respectively). (B) Stem CO₂ efflux (SCE) of dominant and co-dominant stems (grey and black circles, respectively). Vertical bars indicate standard errors of the mean ($n = 25$). Stars indicate significant differences between dominant and co-dominant stems ($P < 0.05$).

The seasonal trend of the SCE was strongly related to T_{air} according to an exponential relationship (Figure 4). Given that the measurements were performed over time, this relationship may also include temporal phenological changes. The 'apparent' Q_{10} values derived from this relationship were 2.59 and 2.34 for co-dominant and dominant trees, respectively. These values are inside the Q_{10} range of the database for SCE rates reported by Damesin et al. (2002). The basal rate of SCE (defined as SCE at 15 °C) was 0.27 and 0.83 $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ for co-dominant and dominant trees, respectively.

Our result confirmed that the seasonal change in SCE could be expressed as a function of T_{air} as reported in other studies (Levy and Jarvis 1998, Damesin et al. 2002). Other factors related to the seasonal variation in temperature, but not

considered in this study, may codetermine seasonal changes in SCE. In particular, the annual cycle of activity and dormancy of the vascular cambium (Vose and Ryan 2002) and the seasonal patterns of TNC concentration in tree stems are important in this regard, because they are related to photosynthetate mobilization and translocation from the stem to support growth and thus stem respiration (as observed at the Collelongo experimental site; Scartazza et al. 2004, 2013).

The amount of carbon released from May 2007 to May 2008 by the SCE, calculated considering the stand structure of the study site was about 63 g C m⁻² year⁻¹. Dominant trees contributed ~70%, despite the fact that the basal area was approximately equally distributed between dominant and co-dominant trees. The estimated annual value is in the range

reported for coniferous forest stands (Ryan et al. 1995, Maseyk et al. 2008) but is much smaller compared with other broad-leaved forests (Edwards and Hanson 1996, Tang et al. 2008), especially beech forests (Damesin et al. 2002). Overall, comparison between different studies is difficult as climate, tree density, age and scaling up methods can vary largely (Damesin et al. 2002). However, the lower values estimated by us can be partly explained by the lack of measurements on branches in our study. The juvenile tissues present on current year beech branches could have a higher density of living cells, higher nitrogen content (Ceschia et al. 2002), more stored carbohydrates and greater carbohydrate translocation (Sprugel 1990), with consequently higher respiration rates from juvenile tissues than older ones. Moreover, some of the CO₂ produced by respiration of plant organs can dissolve in sap and move upward in xylem (Teskey and McGuire 2007, Aubrey and Teskey 2009) and can diffuse to the atmosphere through above ground tissues remote from the site of respiration (Teskey and McGuire 2007) including the thinner-barked branches (Sprugel 1990). All those phenomena could cause higher CO₂ efflux rates from

juvenile branch tissues and, therefore, we may have underestimated the amount of carbon released by the SCE.

Leaf respiration

Most of the leaf parameters examined in this study varied significantly with canopy position (Table 1). The shaded leaves showed a lower LMA than sun leaves ($P = 0.0002$), confirming the observed canopy variation in LMA in relation to irradiance and height within the beech canopy (Matteucci 1998, Montpied et al. 2009). The LMA and C/N ratio values were comparable to the ones coming from the beech sites of the Italian network of permanent monitoring sites CONECOFOR (which includes the Collelongo experimental site) (Bussotti et al. 2005).

The TNC concentration measured in our study is within the range reported for beech and other broad-leaf trees (Landolt and Pfenninger 1997, Griffin et al. 2002, Whitehead et al. 2004, Xu and Griffin 2006, Gavrichkova et al. 2011). The TNC concentration of sun leaves was significantly higher than that measured in shade leaves ($P = 0.004$) even when expressed on a leaf mass basis. This finding is confirmed by the gradually decreasing TNC concentration from the top crown layer to the bottom of the crown observed during a recent study at the same experimental site (Gavrichkova et al. 2011).

Leaf dark respiration rates expressed on a leaf area basis differed significantly between the two canopy layers: the LR rates measured in the sun leaves were higher than those measured in the shade leaves ($P = 0.0005$). This finding is in agreement with previous studies (Griffin et al. 2001, 2002, Turnbull et al. 2003, Whitehead et al. 2004). On average, leaf respiration rates measured at the standard temperature of 15 °C were 0.70 ± 0.08 and $0.30 \pm 0.05 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ for sun and shade leaves, respectively (Table 1). Similar values were reported by De Angelis and De Luca (1998) in a previous study in the same forest (0.50 and $0.25 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ for sun and shade leaves, respectively). Moreover, Griffin et al. (2002) found LR rates measured at 15 °C ranging between 0.62 and $1.38 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$, whereas Xu and Griffin (2006) reported values of LR at 10 °C between 0.51 and $0.64 \text{ CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ for the sun leaves, whereas rates of the shade leaves were between 0.28 and $0.43 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$. Nevertheless, when LR rates were calculated on a leaf mass basis (Table 1), the effect of canopy position was no longer evident, as a consequence of the variation of LMA.

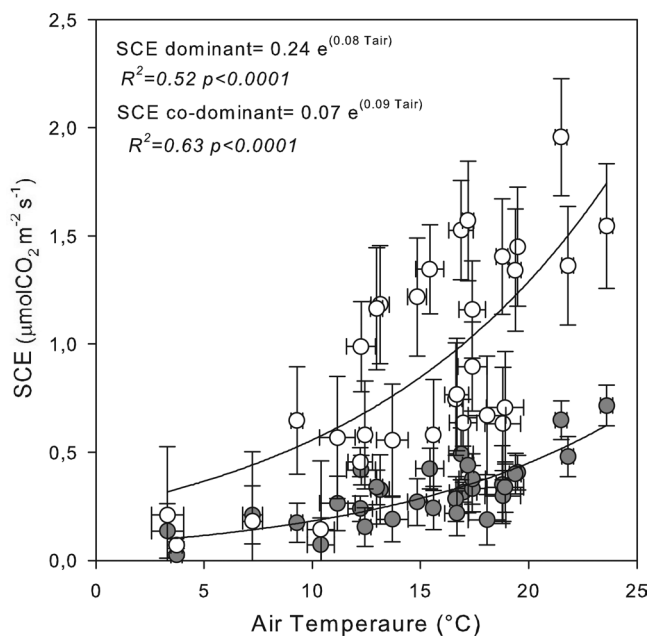


Figure 4. Stem CO₂ effluxes (SCE) of dominant and co-dominant stems (white and grey circles, respectively) as functions of air temperature. Vertical bars indicate standard errors of the mean ($n = 5$).

Table 1. Average values (s.e.) of LR rates ($\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$, $\text{mg CO}_2 \text{ g}^{-1} \text{ h}^{-1}$), LMA (g m^{-2}), nitrogen concentration (N %), carbon concentration (C %), C/N ratio and TNC (g m^{-2}) for sun and shade leaves ($n = 15$). Different letters in the same column indicate significant differences at $P < 0.05$.

	LR		LMA	N	C	C/N	TNC
	$\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$	$\text{mg CO}_2 \text{ g}^{-1} \text{ h}^{-1}$	g m^{-2}	%	%		g m^{-2}
Sun	0.73 (0.08) ^a	1.12 (0.09) ^a	91.07 (6.90) ^a	2.42 (0.08) ^a	49.60 (0.27) ^a	20.63 (0.80) ^a	6.96 (0.46) ^a
Shade	0.30 (0.05) ^b	1.17 (0.12) ^a	38.28 (0.12) ^b	2.58 (0.13) ^a	47.77 (0.16)	18.72 (0.87) ^a	1.79 (0.20) ^b

The TNC were a very good predictor of LR, explaining ~81% of both space and time variability of LR rates (Figure 5). This relationship is probably related to the light environment of leaves; indeed in the experimental site, the upper canopy leaves had higher photosynthetic rates as a result of higher quality and quantity of light (De Angelis and De Luca 1998, Matteucci et al. 1999). In turn, as reported in many other studies, leaves in the upper canopy layer contained more non-structural carbohydrates that support respiratory processes (Azcon-Bieto and Osmond 1983, Griffin et al. 2002, Tissue et al. 2002, Turnbull et al. 2003, Xu and Griffin 2006). As reported for a large number of species (Wright et al. 2004), LR is related to the nitrogen content at site level as well as across plant functional groups and ecosystem types. In this study, the variability of LR did not show any relationship with the N content. The estimated annual amount of carbon released via LR integrated for the whole canopy was $272 \text{ g C m}^{-2} \text{ year}^{-1}$, which is similar to the amount reported in some temperate and boreal forests (Griffis et al. 2004, Gaumont-Guay et al. 2006, Wang et al. 2010), but higher than those reported in other CO_2 flux partitioning studies (Bolstad et al. 2004, Tang et al. 2008, Wieser et al. 2009).

Ecosystem respiration

Based on up-scaled chamber measurements, R_{ECO} showed a significant temporal variation over the study period (Figure 6). For calculation of the partitions among the ecosystem components, coarse woody debris was not included, given that it was negligible at the site, as it is regularly collected by the local

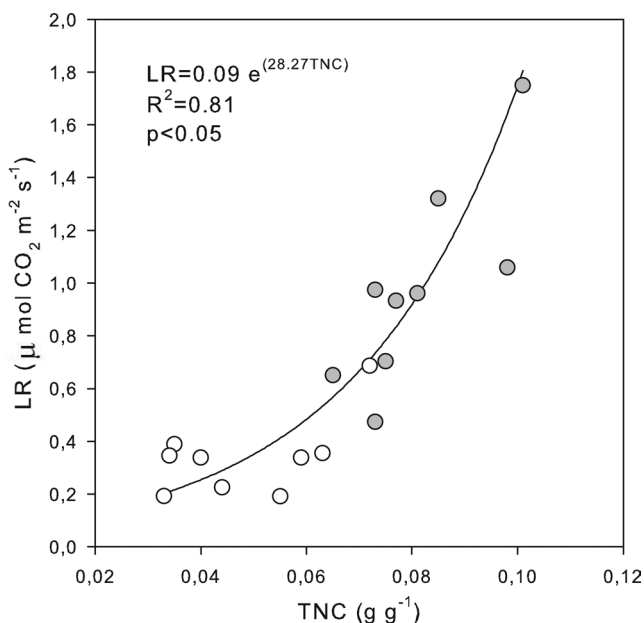


Figure 5. Leaf respiration as a function of TNC. Each data point represents a single measurement of shade and sun leaves (white and grey circles, respectively).

population. Soil CO_2 efflux was the most important component of R_{ECO} during the study period, with a contribution ranging from ~20% in summer to >90% in winter (Figure 6). In contrast, the contributions of SCE and LR were highest in summer, when they accounted for ~15 and 70% of R_{ECO} , respectively (Figure 6). The increase in the contribution of SCE and LR during the summer partially compensated for the reduction of SR caused by low soil moisture (Figure 6). On an annual basis, SR, SCE and LR accounted for 56, 8 and 36% of R_{ECO} , respectively. These results are similar to those presented in other Mediterranean forest types (Maseyk et al. 2008, Wieser et al. 2009), and also in temperate forests (Xu et al. 2001, Khomik et al. 2010, Wang et al. 2010).

The annual amount of carbon released via R_{ECO} estimated by summing up the different components: SR, LR and SCE was $764 \text{ g C m}^{-2} \text{ year}^{-1}$, and was in agreement with the estimated R_{ECO} obtained after partitioning NEE measured by eddy covariance into $R_{\text{ECO-EC}}$ ($714 \text{ g C m}^{-2} \text{ year}^{-1}$). Both values are comparable to the $R_{\text{ECO-EC}}$ reported in previous studies at the same experimental site (Valentini et al. 1996, 2000) and in other beech forests in Europe (Granier et al. 2003).

There was a good agreement between R_{ECO} estimates based on chamber methods and those derived from the eddy-covariance technique measurements, $R_{\text{ECO-EC}}$ ($P < 0.0001$, <10% differences, Figure 6 inset) except for two peaks in summer, when the R_{ECO} was much higher than $R_{\text{ECO-EC}}$, and in autumn where the opposite was true (Figure 6). Concerning the summer peaks, both partial refixation of the CO_2 and the reduction of non-photorespiratory CO_2 release were not considered in this study although it has been reported that these could cause a 15% overestimation of LR in the illuminated leaves (Luyssaert et al. 2009 and the reference therein). In addition, we were unable to assess the summer drought effect on LR, which several studies have found to limit LR (Atkin and Macherel 2009). On the other hand, the underestimation in autumn could be a consequence of the fitting procedure used being unable to predict the sudden pulses typically reported for these environments after a drought period (Jarvis et al. 2007, Unger et al. 2012).

Conclusions

The relative contribution of soil, stem and leaves to the total annual CO_2 efflux was 56, 8 and 36%, respectively, confirming that SR is the main contributor for the annual carbon balance also in Mediterranean beech forest ecosystem (Matteucci et al. 2000).

Ecosystem respiration and its main components showed strong seasonal variability in a beech forest in central Italy. Summer drought played a crucial role in the observed reduction of R_{ECO} , mainly as a consequence of a strong limitation of SR. In contrast, SCE did not respond to the reduction in SWC, increasing over the summer with increasing temperatures.

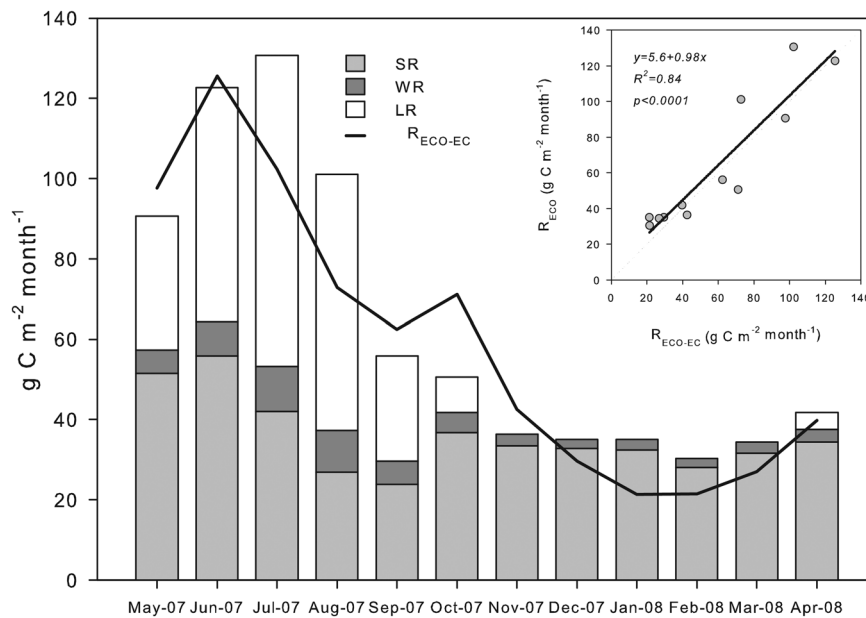


Figure 6. Estimated monthly SR (light grey bars), SCE (dark grey bars) and LR (white bars) during the study period. The black line is the total R_{ECO-EC} during the same period. The small inset graph shows total R_{ECO} estimated by the sum of SR, SCE and LR in comparison with total R_{ECO-EC} . The dotted line is the 1 : 1 line.

Beyond the environmental variables, the CO_2 respiratory flux depended on stand structural variables like the tree social class position (SCE) and the leaf canopy distribution (LR), affecting the resources metabolism and thus the respiratory substrates. Total ecosystem respiration estimated by up-scaled chamber methods and by eddy covariance were in good agreement (difference limited to <10%), indicating that, at least for the study years, this process was reliably measured for the Collelongo beech forest.

Overall, the study constitutes a contribution to increase our understanding of environmental and structural controls of ecosystem respiration, a process that will be crucial in determining the response of forests to global change.

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Conflict of interest

None declared.

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