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Partitioning of ecosystem respiration in a beech forest

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ABSTRACT

Terrestrial ecosystem respiration (R_{eco}) represents a major component of the global carbon cycle. It consists of many sub-components, such as aboveground plant respiration and belowground root and microbial respiration, each of which may respond differently to abiotic factors, and thus to global climate change. To correctly predict future carbon cycles in forest ecosystems, R_{eco} must therefore be partitioned and understood for each of its various components.

In this study we used the eddy covariance technique together with manual and automated closed-chambers to quantify the individual components of R_{eco} in a temperate beech forest at diel, seasonal and annual time scales. R_{eco} was measured by eddy covariance while respiration rates from soil, tree stems and isolated coarse tree roots were measured bi-hourly by an automated closed-chamber system. Soil respiration (R_{soil}) was measured in intact plots, and heterotrophic R_{soil} was measured in trenched plots. Tree stem (R_{stem}) and coarse root (R_{root}) respiration were measured by custom made closed-chambers.

We found that the contribution of R_{stem} to total R_{eco} varied across the year, by only accounting for 6% of R_{eco} during winter and 16% during the summer growing season. In contrast R_{soil} was approximately half of R_{eco} during winter (52%), spring (45%) and summer (49%), while the contribution increased to 79% during autumn.

Based on observed fluxes in the trenched and intact soil plots, we found that autotrophic R_{soil} accounted for 34% of R_{soil} during summer, i.e. a relatively low fractional estimate compared to findings from other studies. It is likely that dead roots were still decomposing in the trenched soil plots thus causing overestimation of heterotrophic R_{soil}.

Diel R_{stem} and R_{root} measurements showed a distinct pattern during summer with the highest respiration rates around 13:00-15:00 CET for R_{stem}, and the highest respiration seen from 9:00–15:00 for R_{root}. In contrast, R_{soil} showed the lowest respiration during daytime with no clear difference in the diel pattern between the intact and trenched soil plots.

Finally, we calculated annual R_{soil} for different transects, and found that annual R_{soil} estimated from the previously used transect at the site was underestimated due to R_{soil} of the transect not being representative for the spatial heterogeneity of R_{soil} at the site. This highlights the importance of performing a sufficient number of chamber measurements at a site to adequately capture the spatial variation and estimate R_{soil} correctly.

1. Introduction

Ecosystem respiration (R_{eco}) is, after gross primary productivity (GPP), the second largest flux of CO_2 between the biosphere and the atmosphere (Beer et al., 2010; IPCC, 2013). R_{eco} is the sum of respiration from several component of the ecosystem that may respond differently to abiotic factors, and thus to global change (Schimel et al., 2001; Valentini et al., 2003). To correctly understand and predict future ecosystem carbon cycles, R_{eco} must therefore be partitioned into its main sub-components. For forests, major components are aboveground autotrophic respiration from the leaves, branches and stems of the trees, and belowground by the autotrophic respiration from tree roots and the heterotrophic respiration from soil microbes, which together form the soil respiration (R_{soil}) (Hanson et al., 2000; Högberg et al., 2005, Rodeghiero and Cescatti, 2006).

Ecosystem-level net atmospheric exchange of CO_2 (NEE) can be measured on a high temporal scale by the eddy covariance method (e.g. Pilegaard et al., 2001; Wofsy et al., 1993). NEE can be partitioned into GPP and R_{eco}, by various extrapolation methods, one of which uses temperature response functions to extrapolate from measured nighttime respiration rates to estimates of daytime respiration (Reichstein et al., 2005). Whereas eddy covariance provides R_{eco} on a high temporal scale,

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it does not provide information on the individual components that make up R_{eco}. Instead, chamber based methods can be used to measure the CO_2 flux from the individual components by enclosing a specific part of the ecosystem in a chamber. Typically, chambers of the closed type are used, where the CO_2 flux is calculated based on the near-linear increase in chamber CO_2 concentration during the measurement. Chamber-based methods differ from the eddy covariance method by the smaller spatial coverage (Wang et al., 2010). Eddy covariance covers a large footprint area that may be representative for the studied ecosystem (Nagy et al., 2006). R_{soil}, however, often show a high degree of spatial heterogeneity within the footprint area (Knohl et al., 2008; Webster et al., 2008). At eddy covariance sites, R_{soil} is often determined with manually operated soil chambers (e.g. Wu et al., 2013). To ensure that R_{soil} measurements are representative for the eddy covariance footprint, a sufficient number of measurements must be performed throughout the footprint (Davidson et al., 2002; Savage et al., 2008). By performing the manual chamber measurements distributed throughout the footprint at regular intervals throughout the year, both the seasonal change in R_{soil} and the spatial difference in R_{soil} can be captured to give a good estimate of R_{soil} for the footprint (Savage and Davidson, 2003). However, because of labour intensiveness, manual measurement campaigns rarely capture diel or day to day variability in the fluxes. Automated chamber systems can allow for measurements at much higher temporal resolution, but because of budget constraints usually only a limited number of automated chambers are available causing low spatial coverage of automatic systems. Apart from R_{soil}, measurements of other ecosystem components such as respiration from leaves, branches and tree stems and woody debris lying on the soil surface have been made using both manual and automated chambers (Rodríguez-Calcerrada et al., 2014; Tang et al., 2008; Zhu et al., 2012). As for R_{soil}, these components can show a high degree of spatial and temporal variability throughout the footprint, thus requiring a sufficient number of chamber measurements to capture this variability.

The diel pattern of R_{soil} is generally related to soil temperature (Janssens and Pilegard, 2003; Tang et al., 2005). However, differences in substrate input of carbon from photosynthesis to the soil via the roots can vary across the day (Kuzyakov and Gavrichkova, 2010). Diel changes in substrate input from plants may completely or partly decouple R_{soil} from the diel pattern of soil temperature (Tang et al., 2005). To study the influence of substrate input and the autotrophic contribution from roots to R_{soil}, a trenching can be performed. Here the contribution of roots to R_{soil} is removed by cutting off any roots in a plot and preventing them to grow back (Baggs, 2006; Bond-Lamberty et al., 2011). This stops autotrophic R_{soil} and prevents any input of carbon from photosynthesis. However, the roots are left to decay in the plot and the soil water content may increase (Díaz-Pinés et al., 2010). By comparing plots with intact soil to plots with trenched soil, the heterotrophic and autotrophic components of R_{soil} can be investigated.

The aim of the study was to quantify the CO_2 fluxes from various components of a forest ecosystem on an annual, seasonal, daily and diel scale, and to quantify how the contribution to total R_{eco} of heterotrophic and autotrophic R_{soil} and stem respiration (R_{stem}) vary on a seasonal scale. This was achieved by a combination of the eddy covariance method and manual and automated closed-chamber techniques.

2. Materials and methods

2.1. Site description

Measurements were performed at the Danish ICOS RI site called DK-Sor at 40 m a.s.l. (55°29′13″ N, 55°38″45″ E), where eddy covariance measurements of net ecosystem CO_2 fluxes have been performed continuously since 1996. The climate is temperate maritime with an annual average precipitation and an annual average temperature of 564 mm and 8.5 °C, respectively (Pilegaard et al., 2011).

The forest is dominated by European beech (*Fagus sylvatica* L.) planted in 1921 with small stands of Norway spruce (*Picea abies* (L.) Karst) and European larch (*Larix decidua* Mill.) (Wu et al., 2013). The tree stem density is 288 per hectare with an average tree height of 28 m and an average diameter at breast height (DBH) of 42 cm in 2010. The main rooting depth is 1 m (Pilegaard et al. 2011). However, roots are most frequent at a depth of 0–20 cm (Østergård, 2000). The dense canopy has a peak LAI of 5.0 and the average annual canopy cover duration period is 180 days. The understory is poorly developed due to the well-developed canopy, causing a sparsely vegetated forest floor during most of the year, except during spring when wood anemones (*Anemone nemorosa* L.) are present in part of the forest floor. Depending on the base saturation, the soils are classified as either alfisols or mollisols. The soil carbon pool is 20 kg m^{-2} down to 1 m depth, with a C/N ratio of 20 in the upper organic soil layers, decreasing to 10 in the lower mineral layers (Østergård, 2000). The organic layer is 10–40 cm deep (Pilegaard et al., 2001).

2.2. Eddy covariance measurements

Measurements of NEE were performed at a height of 43 m on the flux tower on the site by a closed-path eddy covariance system based on a Gill HS-50 3D research sonic anemometer (Gill Instruments Limited, Lymington, UK) and a fast response infrared gas analyser LI-7000 (LI-COR Environmental, Lincoln, Nebraska, USA). For details on the raw data processing, see Pilegaard et al., (2011). Nighttime fluxes at insufficient turbulent mixing were removed when the friction velocity (u_*) was lower than 0.1 m s^{-1} and the atmospheric stratification was stable. A dead band of 2 h after re-establishment of turbulent conditions was applied to avoid double accounting from measuring CO_2 fluxes from venting the canopy air space. The removal of data below the u_* threshold value, and periods of system failure, resulted in a data coverage of 54.1% for 2016. The data set was gap-filled and NEE was partitioned into GPP and R_{eco} by the online "REddyProc: Eddy covariance data processing tool" (Department of Biogeochemical Integration, MPI Jena (2017)). In short, the gap-filling procedure follows the approach by Reichstein et al. (2005), and the partitioning of NEE follows the look-up table approach by Reichstein et al. (2005) and the regression approach by Lasslop et al. (2010). This resulted in a continuous data set of half-hourly values of NEE, GPP and R_{eco} for the entire year. From the half-hourly values, the mean daily values were calculated as well as monthly and annual sums of NEE, GPP and R_{eco}.

For the each of the annual sums of NEE, GPP and R_{eco} an uncertainty estimate was calculated. Wu et al. (2013) used five years of data to calculate the relative uncertainties of the annual sums of NEE, GPP and R_{eco} for the DK-Sor site by taking the uncertainties caused by u_* filtering, gapfilling and site heterogeneity into account. By using these relative uncertainties, we calculated the uncertainty estimates for the annual sums of NEE, GPP and R_{eco}.

2.3. Manual closed-chamber soil respiration measurements

R_{soil} was measured manually using a portable 8100-102 10 cm survey chamber connected to a LI-8100A Automated Soil CO_2 Flux System (LI-COR Environmental, Lincoln, Nebraska, USA). R_{soil} was measured on permanently installed soil collars, inserted 4 cm into the soil, on three distinct transects in the footprint area of the eddy covariance measurements. The R_{soil} plots contained litter but no living plants. The first transect, called the inside fence transect, consisted of 12 plots that were positioned within 15 m of the flux tower. The second transect, called the south transect, consisted of 27 plots, which were positioned at 9 locations along a straight line starting 30 m from the flux tower and ending 270 m south of the tower. Each of the 9 locations contained 3 R_{soil} plots. The last transect, called the west transect, consisted of 45 plots. The plots were positioned in groups of three at 15 locations along two parallel lines that were separated by 30 m. The lines started 30 m from the flux tower and ended 210 m to the west. The