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Title

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.

Keywords: Ecosystem respiration, flux partitioning, eddy covariance, chamber, seasonality

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,

48 and thus to global change (Schimel et al., 2001; Valentini et al., 2003). To correctly understand and
49 predict future ecosystem carbon cycles, R_{eco} must therefore be partitioned into its main sub-
50 components. For forests, major components are aboveground autotrophic respiration from the
51 leaves, branches and stems of the trees, and belowground by the autotrophic respiration from tree
52 roots and the heterotrophic respiration from soil microbes, which together form the soil respiration
53 (R_{soil}) (Hanson et al., 2000; Högberg et al. 2005, Rodeghiero and Cescatti, 2006).

54 Ecosystem-level net atmospheric exchange of CO_2 (NEE) can be measured on a high temporal
55 scale by the eddy covariance method (e.g. Pilegaard et al., 2001; Wofsy et al., 1993). NEE can be
56 partitioned into GPP and R_{eco} , by various extrapolation methods, one of which uses temperature
57 response functions to extrapolate from measured nighttime respiration rates to estimates of daytime
58 respiration (Reichstein et al., 2005). Whereas eddy covariance provides R_{eco} on a high temporal
59 scale, it does not provide information on the individual components that make up R_{eco} . Instead,
60 chamber based methods can be used to measure the CO_2 flux from the individual components by
61 enclosing a specific part of the ecosystem in a chamber. Typically, chambers of the closed type are
62 used, where the CO_2 flux is calculated based on the near-linear increase in chamber CO_2
63 concentration during the measurement. Chamber-based methods differ from the eddy covariance
64 method by the smaller spatial coverage (Wang et al., 2010). Eddy covariance covers a large
65 footprint area that may be representative for the studied ecosystem (Nagy et al., 2006). R_{soil} ,
66 however, often show a high degree of spatial heterogeneity within the footprint area (Knohl et al.,
67 2008; Webster et al., 2008). At eddy covariance sites, R_{soil} is often determined with manually
68 operated soil chambers (e.g. Wu et al., 2013). To ensure that R_{soil} measurements are representative
69 for the eddy covariance footprint, a sufficient number of measurements must be performed
70 throughout the footprint (Davidson et al., 2002; Savage et al., 2008). By performing the manual
71 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 CO₂ 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 CO₂ 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, 2001). 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, 2001). The organic layer is 10–40 cm deep (Pilegaard et al. 2001).

2.2 Eddy covariance measurements

120 Measurements of NEE were performed at a height of 43 m on the flux tower on the site by a closed-
 121 path eddy covariance system based on a Gill HS-50 3D research sonic anemometer (Gill
 122 Instruments Limited, Lymington, UK) and a fast response infrared gas analyser LI-7000 (LI-COR
 123 Environmental, Lincoln, Nebraska, USA). For details on the raw data processing, see Pilegaard et
 124 al. (2011). Nighttime fluxes at insufficient turbulent mixing were removed when the friction
 125 velocity (u_*) was lower than 0.1 m s^{-1} and the atmospheric stratification was stable. A dead band of
 126 2 hours after re-establishment of turbulent conditions was applied to avoid double accounting from
 127 measuring CO_2 fluxes from venting the canopy air space. The removal of data below the u_*
 128 threshold value, and periods of system failure, resulted in a data coverage of 54.1 % for 2016. The
 129 data set was gap-filled and NEE was partitioned into GPP and R_{eco} by the online "REddyProc: Eddy
 130 covariance data processing tool" (Department of Biogeochemical Integration, MPI Jena). In short,
 131 the gap-filling procedure follows the approach by Reichstein et al. (2005), and the partitioning of
 132 NEE follows the look-up table approach by Reichstein et al. (2005) and the regression approach by
 133 Lasslop et al. (2010). This resulted in a continuous data set of half-hourly values of NEE, GPP and
 134 R_{eco} for the entire year. From the half-hourly values, the mean daily values were calculated as well
 135 as monthly and annual sums of NEE, GPP and R_{eco} .
 136 For the each of the annual sums of NEE, GPP and R_{eco} an uncertainty estimate was calculated. Wu
 137 et al. (2013) used five years of data to calculate the relative uncertainties of the annual sums of
 138 NEE, GPP and R_{eco} for the DK-Sor site by taking the uncertainties caused by u_* filtering, gapfilling
 139 and site heterogeneity into account. By using these relative uncertainties, we calculated the
 140 uncertainty estimates for the annual sums of NEE, GPP and R_{eco} .

141

142 **2.3 Manual closed-chamber soil respiration measurements**

143 R_{soil} was measured manually using a portable 8100-102 10 cm survey chamber connected to a LI-
144 8100A Automated Soil CO₂ Flux System (LI-COR Environmental, Lincoln, Nebraska, USA). R_{soil}
145 was measured on permanently installed soil collars, inserted 4 cm into the soil, on three distinct
146 transects in the footprint area of the eddy covariance measurements. The R_{soil} plots contained litter
147 but no living plants. The first transect, called the inside fence transect, consisted of 12 plots that
148 were positioned within 15 m of the flux tower. The second transect, called the south transect,
149 consisted of 27 plots, which were positioned at 9 locations along a straight line starting 30 m from
150 the flux tower and ending 270 m south of the tower. Each of the 9 locations contained 3 R_{soil} plots.
151 The last transect, called the west transect, consisted of 45 plots. The plots were positioned in groups
152 of three at 15 locations along two parallel lines that were separated by 30 meters. The lines started
153 30 m from the flux tower and ended 210 m to the west. The location for the south and west transects
154 were chosen to be in the main wind directions and source area for the eddy covariance
155 measurement. See Pilegaard et al. (2011) and Wu et al. (2013) for information about the footprint
156 area and wind direction at the site.

157 The manual measurements were performed at an interval of two to three weeks, where R_{soil} was
158 measured once per plot with a chamber closure time of 150 seconds. This resulted in 20 campaign
159 measurements evenly distributed in time during 2016 for each of the transects. The measurements
160 of the three transects were typically performed on two adjacent days between 09:00–16:00 CET,
161 with the inside fence and south transect being measured on the first day, and the west transect being
162 measured on the second day.

163

164 **2.4 Automated closed-chamber measurements**

165 In addition to the manual chamber measurements, automated closed-chamber measurements of
166 respiration from intact soil, trenched soil, coarse roots and tree stems were performed from 4

167 January 2016 to 31 December 2016 with a LI-8100A Automated Soil CO₂ Flux System connected
168 to a LI-8150 Multiplexer (LI-COR Environmental, Lincoln, Nebraska, USA). All the automated
169 soil, root and stem chambers were positioned within 15 m from the flux tower. The system
170 performed well through the entire measurement period leading to automatic measurement being
171 performed each day.

172 R_{soil} was measured by six opaque soil chambers on circular soil collars with a diameter of 20 cm
173 that were permanently inserted 4 cm into the soil. The soil collars contained soil and litter but no
174 aboveground plant parts. One of the soil chambers was an 8100-101 Long-Term CO₂ flux
175 chambers, and five were 8100-104 Long-Term CO₂ flux chambers (LI-COR Environmental,
176 Lincoln, Nebraska, USA). For two of the soil chambers, trenching was first performed on 6 April
177 2016 to remove the contribution of living roots to the total R_{soil} from the plot. The trenching was
178 done by vertically inserting a spade 25 cm into the soil in a circle around the soil chambers. Roots
179 with a diameter too big to be cut with the spade were cut with a saw. To prevent ingrowth of roots,
180 monthly re-trenching was performed throughout the study period. Thus, the six soil chamber plots
181 consisted of two trenched soil plots and four intact soil plots.

182 R_{stem} and R_{root} were measured with two custom made coarse root chambers and two custom made
183 stem chambers, respectively. Unlike the LI-COR soil chambers, the root and stem chambers did not
184 open between measurements. Instead, the chamber headspace was continuously flushed between
185 measurements with atmospheric air that was let into the chamber by a small tube. The flow of air to
186 all root and stem chambers was provided by a pump, and the flow to each chamber set to 1 L min⁻¹
187 by a flow meter. This resulted in a near ambient atmospheric air CO₂ concentration in the chambers
188 between measurements. At the beginning of a chamber measurement, the flow of air to the specific
189 chamber was stopped by automatically closing a normally open solenoid valve that was placed on
190 the flush tube going to the chamber. Thus, the chambers were closed during measurements.

191 The two root chambers were made of transparent acrylic glass and were cylindrical in shape with an
192 inner length of 24 cm and an inner diameter of 7 cm giving a volume of 923 cm³. Before assembly
193 the cylinder was cut in two halves in the longitudinal axis. A 10 cm long tube with an inner
194 diameter of 0.5 cm, and a filter in the end was attached to the chamber, which acted as a vent to the
195 atmosphere. The chambers were installed in June 2015. For each chamber a suitable coarse root
196 from a soil depth of 5-10 cm was carefully exposed, and the root was rinsed by tap water. The
197 diameter of root was measured, and the root volume and root surface area was calculated. The root
198 was placed in the one half of the cylinder and the other half of the cylinder was placed on top. In
199 each end of the cylinder, the root went through a hole. The two half cylinders were sealed to each
200 other and the hole around the root in each end was sealed with Blu-tack. Following this, the
201 chamber was covered with soil.

202 The two stem chambers were cylindrical and made of polypropylene, with an inner diameter of 15
203 cm and an inner height of 10 cm, giving a volume of 1757 cm². A 10 cm vent tube with an inner
204 diameter of 0.5 cm, and a filter in the end was attached at the bottom of the chamber. The chambers
205 were attached to the smooth stem surfaces of two beech trees at a height of 1.3 m by a rubber
206 extrusion with a u-profile that was attached to the chamber and sealed with silicone. The chamber
207 was held in place on the stem by adjustable straps.

208 The ten chambers were connected to the LI-8100A/ LI-8150 in a multiplexed setup, and the system
209 was set up in a repeated automated two-hour cycle during which a measurement of each of the soil,
210 root and stem chambers was performed. The chamber closure time was set to 5 minutes and the pre-
211 purge and post-purge times were set to 40 seconds for all chambers.

212

213 **2.5 Chamber flux calculation and up-scaling of fluxes**

214 All data analysis of the chamber based CO₂ fluxes and post-processing of the eddy covariance data
 215 was done using R version 3.2.0 (R Core Team, 2014).
 216 CO₂ fluxes for all chamber measurements were calculated for each individual measurement on a
 217 time and area basis by fitting the non-linear equation by Hutchinson and Mosier (1981) with the
 218 nlsLM function (minpack.lm package) for model fitting in R (Elzhov et al. 2015). For the manual
 219 chamber measurements, the first 20 seconds after chamber closure were discarded from the flux
 220 calculation (the dead band), whereas the dead band was set to 100 seconds for the automated
 221 chamber measurements because an external analyser (used in another study) was attached in
 222 parallel with the LI-8100/LI-8150 system, causing increased system volume and therefore increased
 223 system response time.
 224 The calculated automated chamber fluxes from soil, stem and coarse roots were quality flagged first
 225 by removing fluxes with an $r^2 < 0.80$ of the fit. Following this, the automated soil fluxes, but not
 226 stem and root fluxes, were further quality flagged by removing measurements performed at low u_* ,
 227 where soil fluxes measured by the LI-8100A/LI-8150 system at the site have been found to be
 228 overestimated (Brændholt et al. 2017). In short, the automated soil chamber fluxes were compared
 229 with u_* measured at the flux tower. From a plot of the fluxes against u_* , a threshold value of 0.2 m
 230 s⁻¹ was determined visually, as where the decrease of fluxes in response to an increase in u_* levelled
 231 off. Fluxes below the u_* threshold value were removed from further analysis. In total the quality
 232 control removed 16.3 % of the automated root and stem chamber measurements and 44.9 % of the
 233 automated soil chamber measurements, leaving 30124 automated chamber measurements for
 234 further analysis. For the manual chamber measurements no quality control was applied in the post
 235 processing. Instead the quality control was done in the field following a measurement. If the
 236 coefficient of variance of the flux, provided by the LI-COR software, was higher than 1.4 %, the
 237 measurement was discarded and an extra measurement was performed on the plot.

From the quality controlled flux chamber measurements different estimates for the annual CO₂ fluxes were calculated for both the manual and automated measurements following the procedure described by Brændholt et al. (2017). For the manual measurements, annual soil CO₂ fluxes were calculated both for the inside fence transect, the south transect and the west transect. For each transect, the manual fluxes were used to parameterize an empirical model of R_{soil} as a function of soil temperature as described by Lloyd and Taylor (1994):

$$R_s = R_{283} \exp \left[-E_0 \left(\frac{1}{T_s + 273.15 - T_0} - \frac{1}{T_s - T_0} \right) \right], \quad (1)$$

where T_0 and E_0 are fitted parameters, T_s is soil temperature measured at 5 cm depth and R_{283} is the base respiration at a soil temperature of 10 °C. The model was fitted with nlsLM in the R package minpack.lm (Elzhov et al. 2015) that uses a nonlinear least squares regression based on a Levenberg–Marquardt algorithm. By using soil temperature at 5 cm depth measured continuously at the site as model driver input, a continuous one-year time series of mean daily R_{soil} was calculated. A potential soil temperature bias could occur if the soil temperature continuously measured inside the fence at the site, which was used for modelling of the annual CO₂ fluxes, systematically differed from the soil temperatures of the manually measured soil respiration plots. However, no systematic soil temperature difference was found, e.g. exemplified by a mean annual soil temperature inside the fence of 8.4 °C compared to mean annual soil temperatures of 8.7 and 8.2 °C for the south transect and west transect, respectively.

For the automated measurements, annual mean CO₂ fluxes were calculated for the four intact soil plots, the two trenched soil plots, the two root plots and the two stem plots, respectively. Each of the annual CO₂ fluxes was calculated by first averaging the bi-hourly fluxes on a monthly basis, providing a diel pattern of fluxes for each month. From this, a daily mean flux was calculated on a

262 monthly basis at the average of the bi-hourly values. Monthly fluxes were calculated as the sum of
263 the daily soil fluxes in the respective month, and the annual flux was calculated as the sum of the 12
264 months.

265 The uncertainties of the annual soil CO₂ fluxes based on the manual chamber for each of the three
266 transects were estimated by the approach used in Wu et al. (2013), which is based on Van Oijen et
267 al., (2005). In short, for each transect a Bayesian calibration was used to quantify the uncertainty of
268 the model predictions, for which a Markov Chain Monte Carlo (MCMC) Metropolis-Hastings
269 random walk algorithm was used. We performed 50000 MCMC iterations from which the prior
270 parameter distributions were sampled. Different annual soil CO₂ fluxes were calculated using the
271 estimated posterior parameter distributions, and the standard deviation of the annual soil CO₂ fluxes
272 was interpreted as the uncertainty of the annual soil CO₂ flux for a given transect.

273 R_{stem} , calculated on a stem surface area, was scaled up to the soil surface area by using site data on
274 tree density, tree height and DBH. The tree height and DBH were measured for 54 beech trees
275 during March 2017. For each of the measured trees, the surface stem area was calculated as the
276 surface area of a cylinder with the measured height and a diameter of 0.71 times the measured
277 DBH. This diameter was derived from a form factor for European beech that describes the
278 relationship between the stem ground area at breast height and the volume of wood contained in the
279 stem and branches above a diameter of 5 cm (Landesverwaltungsamt Sachsen-Anhalt). The average
280 stem surface area calculated from the sampled trees was multiplied with the tree density of 288
281 stems ha⁻¹ to get the stem surface area scaled on a soil surface area. From this the measured R_{stem} on
282 a stem surface area could be converted to a CO₂ flux on a soil surface area.

283 The uncertainties of the annual soil CO₂ fluxes for the intact soil, trenched and stem measured by
284 the automated chamber were estimated by formal error propagation that took the uncertainties of the
285 various steps in the calculation of the annual fluxes into account. For the annual stem flux, an extra

level of uncertainty was included in the calculation that accounted for the uncertainty of the up-scaling of the fluxes from stem surface area to soil surface area. For this, we assumed an uncertainty of 30 % in the stem surface area calculated from the measurements of tree height and DBH.

3 Results

3.1 Annual CO₂ budgets

Different annual CO₂ budgets were calculated for different components of the forest from both the tower based eddy covariance and the automated and manual closed-chamber measurements.

The gap-filled annual NEE calculated from the eddy covariance measurement at a height at 43 m on the flux tower was $-391 \pm 63 \text{ g C m}^{-2} \text{ yr}^{-1}$, and the estimated GPP and R_{eco} were 2272 ± 136 and $1882 \pm 301 \text{ g C m}^{-2} \text{ yr}^{-1}$, respectively (Fig. 1).

Different estimates of annual R_{soil} were calculated based on the manual closed-chamber measurements that were used to parameterize the Lloyd and Taylor model (Fig. 1). The lowest annual R_{soil} of $794 \pm 51 \text{ g C m}^{-2} \text{ yr}^{-1}$ was found for the inside fence transect, where the plots were positioned within a distance of 15 m from the eddy flux tower. The annual R_{soil} from the two transects, with soil plots distributed in the forest, were both higher with an annual R_{soil} of $1024 \pm 89 \text{ g C m}^{-2} \text{ yr}^{-1}$ for the west transect and an annual R_{soil} of $972 \pm 90 \text{ g C m}^{-2} \text{ yr}^{-1}$ for the south transect.

The average annual R_{soil} based on the automated closed-chamber measurements every two hours was $597 \pm 93 \text{ g C m}^{-2} \text{ yr}^{-1}$ for the four automated chambers with intact soil and, while the average annual R_{soil} for the two automated chambers containing trenched soil was $375 \pm 29 \text{ g C m}^{-2} \text{ yr}^{-1}$, accounting for 63 % of R_{soil} for the intact soil plots.

The annual up-scaled stem CO₂ on a soil surface area basis was 264 ± 88 and $191 \pm 64 \text{ g C m}^{-2} \text{ yr}^{-1}$ for the two automated stem chambers, respectively, resulting in an average of $227 \pm 108 \text{ g C m}^{-2} \text{ yr}^{-1}$ (Fig. 1). This was equivalent to $258 \pm 15 \text{ g C m}^{-2} \text{ yr}^{-1}$ on a stem surface area basis.

310 Compared to the annual estimate of R_{eco} from the eddy covariance measurements, the annual R_{soil}
311 constituted 43, 55 and 52 % from the manually measured inside fence transect, the west transect and
312 the south transect, respectively, while the annual R_{soil} based in the intact soil plots and trenched soil
313 plots measured automatically constituted 32 and 20 % of R_{eco} , respectively. The average stem CO_2
314 flux constituted 12 % of R_{eco} .

315

316 **3.2 Seasonal forest respiration**

317 R_{eco} , R_{soil} and R_{stem} generally followed the same pattern throughout the year with the lowest
318 respiration rates during the cold winter months and the highest rates during the warm summer
319 months (Fig. 2, Fig. 3). However, the individual contribution of R_{soil} and R_{stem} to the total R_{eco}
320 differed between the seasons. R_{stem} showed a high seasonality in its contribution to the total R_{eco}
321 contributing only 6 % of R_{eco} during the winter months of January, February and December. A
322 similar low contribution of 7 % was seen during the spring months of March, April and May.
323 However, during the summer months of June, July and August the contribution of R_{stem} increased to
324 16 %. In the autumn months of September, October and November the contribution gradually
325 decreased from 16 % in September to a level of 9 % in November, close to the winter level. The
326 monthly pattern of contribution of R_{soil} to the total R_{eco} differed from R_{stem} . Here winter, spring and
327 summer were fairly similar contributing 52, 45 and 49 % to R_{eco} , respectively. However, R_{soil} during
328 the autumn months differed from the rest of the year by contributing 79 % to the total R_{eco} .
329 R_{root} , which was measured for two coarse roots, was not scaled up to the soil surface area because of
330 the various contributions of roots of different sizes to total root respiration.

331

332 **3.3 Effect of trenching**

333 The annual average R_{soil} for the two trenched soil plots measured by the automated chambers was
334 63 % of annual average R_{soil} for the four intact soil plots. However, the trenching was not performed
335 until 5 April 2016. To investigate the effect of the trenching on R_{soil} , we looked at R_{soil} before and
336 after the trenching. Before the trenching R_{soil} of the trenched plots was 77 % of the R_{soil} for the
337 intact soil. However, for the remaining part of the year following the trenching, R_{soil} for the trenched
338 plots decreased to 61 % of the intact soil plots.

339 The course of R_{soil} generally followed the same pattern throughout the year for both the intact and
340 trenched soil plots, by following changes in soil temperature (Fig. 3). However, during the months
341 of June, July and August where GPP was highest (Fig. 4), the intact soil plots reached higher levels
342 of R_{soil} with R_{soil} of the trenched soil plots only being 51 % of the intact plots. R_{soil} of one of the
343 intact soil plots differed by showing a rapid increase in R_{soil} during April and May, but then
344 decreasing again to a level similar to the remaining intact soil plots (Fig. 3). For October, November
345 and December during autumn and winter, where GPP was low to near zero $\mu\text{mol m}^{-2} \text{s}^{-1}$, R_{soil} of the
346 intact soil plots decreased to almost the level of the trenched soil plots, with R_{soil} of the trenched
347 plots being 83 % of the intact plot, a higher level than the pre-trenching level of 77 %.

348

349 **3.4 Stem respiration and GPP**

350 A rapid increase in GPP was seen in May following the leaf out of the deciduous beech trees (Fig.
351 4). GPP peaked in June and the high GPP continued into July, following by lower GPP in August
352 and September. A similar rapid increase in May was not seen for the two R_{stem} plots. Instead, a
353 slower increase was seen in May followed by a peak in R_{stem} in July and August. During autumn,
354 however, the decrease in R_{stem} did seem to follow the decrease in GPP. Instead of following GPP,
355 the course of R_{stem} followed the course of R_{soil} during spring, summer and autumn (Fig. 4). However,
356 during summer a higher day to day variability was seen for R_{soil} compared to R_{stem} .

358 3.5 Diel patterns of CO₂ fluxes

359 The automated chamber measurements performed every two hours throughout the year allowed for
360 investigating the diel patterns of R_{stem} , R_{root} and R_{soil} for both the trenched and intact soil plots for
361 the different seasons of the year (Fig. 5).

362 Although R_{soil} was higher for the intact soil plots than for the trenched plots, the diel pattern of R_{soil}
363 generally exhibited the same pattern for both the intact (Fig. 5a, b, c, d) and the trenched soil plots
364 (Fig. 5a, b, c, d). During winter, R_{soil} was generally higher during daytime than during nighttime.
365 For spring and autumn, however, no clear diel pattern was observed. Summer exhibited a diel
366 pattern with generally low R_{soil} during daytime. A peak in R_{soil} was seen early in the morning and
367 late in the evening before midnight. The diel patterns of R_{stem} and R_{root} during summer differed from
368 R_{soil} by having the highest respiration rates during daytime (Fig. 5k, o). R_{stem} peaked at 13:00-15:00
369 CET, while a longer peak period from 9:00-15:00 was seen for R_{root} . For winter and autumn, no diel
370 pattern was seen for R_{root} (Fig. 5i, l). However, during spring, a similar diel pattern as during
371 summer with highest R_{root} during daytime was observed. The diel pattern of R_{stem} during spring and
372 autumn was similar to the diel pattern during summer, although less pronounced, with highest R_{stem}
373 during daytime. R_{stem} for winter, however, showed no diel pattern, which was in contrast to the high
374 daytime R_{stem} seen during the rest of the year.

375 Soil temperature at 5 cm depth generally showed no diel pattern during winter, summer and autumn
376 (Fig. 6). During spring, however, a moderate diel pattern was observed with highest soil
377 temperatures late in the afternoon or early in the evening and the lowest soil temperatures in the
378 morning. The difference between the highest and lowest diel temperature was, however, only
379 approximately 1 °C.

380

381 4 Discussion

382 4.1 Annual R_{soil} at different transects

383 We measured R_{soil} at three different transects, which revealed that the annual R_{soil} measured on the
384 inside fence transect was 20 % lower than the average annual R_{soil} measured on the west and south
385 transects. Manual R_{soil} measurements on the inside fence transect have previously been used on the
386 site to estimate annual R_{soil} . Wu et al. 2013 found an average annual R_{soil} of $752 \pm 30 \text{ g C m}^{-2} \text{ yr}^{-1}$
387 for a 5 year period, which is close to the 794 ± 51 found in this study. They calculated the
388 aboveground autotrophic respiration to $872 \text{ g C m}^{-2} \text{ yr}^{-1}$, which they found to be unexpectedly high.
389 They argued that it could be explained if R_{soil} had been underestimated, due to the plots having
390 lower R_{soil} than the average R_{soil} of the footprint. The inside fence transect consisted of 12 plots all
391 positioned within 15 meter of the flux tower, at a relatively dry and high ground. In contrast, the
392 two newly established west and south transects, not used in Wu et al. (2013), consisted of 27 and 45
393 plots, respectively, that were spread out evenly in the forest. R_{soil} and soil moisture measured at both
394 transects showed a higher variation than R_{soil} and soil moisture measured at the inside fence transect
395 (Data not shown). Thus, we argue that the two new transects better represent the spatial variation of
396 R_{soil} in the eddy covariance footprint than the inside fence transect. The annual R_{soil} for the two
397 transects were, however, also similar (972 ± 90 and $1024 \pm 89 \text{ g C m}^{-2} \text{ yr}^{-1}$), constituting 53 % of
398 R_{eco} . Knohl et al. (2008) recommended using at least 8 measurement locations spaced randomly
399 throughout the area of interest to get a representative estimate of R_{soil} with sufficient confidence.
400 The two new transects contained 9 and 15 locations throughout the eddy covariance footprint,
401 respectively, each location containing 3 soil collars. Thus, measuring R_{soil} on only one of these
402 transects might be sufficient to cover the spatial variability and get a solid estimation of R_{soil} . The
403 minor difference between the annual R_{soil} from the two transects also supports this. In contrast, the

12 soil collars in the inside fence transect only cover 1 location because they are placed closely together, and therefore do not live up to the recommendations by Knohl et al. (2008). If the new transects had been used in Wu et al. (2013), the higher R_{soil} would have changed the extremely high estimate of aboveground autotrophic respiration. If we correct R_{soil} in Wu et al. based on the relationship between R_{soil} of the inside fence transect and the other two transects in this study, then the annual R_{soil} increases from 752 to 945 $\text{C m}^{-2} \text{ yr}^{-1}$. This in turn would lower the estimate of aboveground autotrophic respiration from 872 to 679 $\text{g C m}^{-2} \text{ yr}^{-1}$, and make the estimates of above and belowground autotrophic respiration more similar as would be expected (Wu et al. 2013).

The annual R_{soil} based on the automated closed-chamber measurements on the 4 intact soil plots was $597 \pm 93 \text{ g C m}^{-2} \text{ yr}^{-1}$, lower than annual R_{soil} of the 3 transects measured by manual chambers. The automated measurements were performed within 15 m from the flux tower, close to the 12 plots of the inside fence transect. Thus, a somewhat similar annual R_{soil} could be expected. However, the annual R_{soil} of the inside transect was $794 \pm 51 \text{ g C m}^{-2} \text{ yr}^{-1}$, higher than the annual R_{soil} based on the automated measurements. The cause for the difference in R_{soil} is unknown. Even though the plots are positioned close to each other, it is possible that spatial heterogeneity within a few metres have caused the difference in R_{soil} . Another possibility is the different closed-chamber systems used, that potentially could lead to different absolute flux values. Lastly, it is possible that the difference between the day time only measurements for the manual chambers and the measurements every two hours for the automated chambers have caused the difference in R_{soil} .

424

4.2 Comparison of annual respiration

GPP was found to be $2272 \pm 136 \text{ g C m}^{-2} \text{ yr}^{-1}$ (Fig. 1). This is high compared to the average of $1881 \pm 127 \text{ g C m}^{-2} \text{ yr}^{-1}$ that has previously been found for the site (Wu et al. 2013). We expect an

428 optimal growing season during the study period to be part of the reason for this. No summer
 429 drought was observed, which has been found to lower forest growth during summer, thus lowering
 430 annual GPP (Ciais et al., 2005). The trees could therefore continue to photosynthesize without any
 431 edaphic or climatic reduction during summer. Furthermore, September was exceptionally warm,
 432 which allowed the trees to continue photosynthesizing for an additional period at high rates (Fig. 4).
 433 R_{eco} was found to be high as well at $1882 \pm 301 \text{ g C m}^{-2} \text{ yr}^{-1}$, which is to be expected due to the
 434 commonly found link between GPP and R_{eco} (Mahecha et al., 2010; Peichl et al., 2013) and higher
 435 than the $1624 \pm 201 \text{ g C m}^{-2} \text{ yr}^{-1}$ found by Wu et al. (2013). Luyssaert et al. (2007) assembled a
 436 global database of GPP and R_{eco} and reported the average GPP and R_{eco} to be 1375 ± 56 and $1048 \pm$
 437 64 , respectively, for temperate humid deciduous forests, which is much lower than found for the
 438 DK-Sor forest. However, we expect GPP and R_{eco} for the DK-Sor forest to be higher because the
 439 forest is at its main productive phase with a uniform stand of 100 year-old beech trees with high
 440 LAI and a fertile soil. Furthermore, the mild maritime climate and the moderately high latitude
 441 close to the northern margin of beech forest's geographic range have relatively long days during the
 442 vegetation period. With a canopy process model, Ibrom et al. (2006) showed for two different
 443 conifer canopies that the northern, maritime climate in Scotland increased the photosynthetically
 444 active radiation use efficiency by 13-14 % compared to a more continental climate at a forest site in
 445 Central Germany. The reason was longer day lengths, a higher fraction of diffuse radiation and
 446 lower vapour pressure deficit at the Scottish site. Compared to the main beech distribution area with
 447 many drier and more continental sites, we conclude that the site conditions at the DK-Sor beech
 448 forest site allow for comparably high forest productivity.
 449 We found an average annual R_{stem} per unit ground area of $227 \pm 108 \text{ g C m}^{-2} \text{ yr}^{-1}$, which is the first
 450 estimate for this flux component at this site (Fig. 1). The quantification of the CO_2 flux from tree
 451 stems has not received the same attention as e.g. R_{soil} and R_{eco} , probably associated with the extra

452 work and cost required to construct and operate the custom made stem chambers, and the
 453 complications to upscale the measurements to the total stand level. R_{stem} can, however, be a
 454 substantial part of R_{eco} , and constituted 12 % of R_{eco} in our study. A few studies have addressed the
 455 role of R_{stem} for different forest ecosystems (Ceschia et al., 2002; Edwards and Hanson, 1996;
 456 Inoue, 2004; Saveyn et al., 2007; Yang et al., 2015; Zha et al., 2004), and a few studies have looked
 457 at R_{stem} for beech trees (Ceschia et al., 2002; Damesin et al., 2012; Saveyn et al., 2007). Tang et al.
 458 (2008) found that R_{stem} accounted for 13 % of R_{eco} in a temperate old-growth hardwood forest in the
 459 USA, close to the findings for our forest. Damesin et al. (2002) measured respiration from stem and
 460 branches and estimated the annual respiration to be between 325 and 383 g C m⁻² yr⁻¹, with R_{stem}
 461 accounting for approximately 50 %. In a review of 18 European forests, Janssens et al. (2000) found
 462 that aboveground respiration accounted for 31 % of R_{eco} . If half of the aboveground respiration is
 463 accounted for by R_{stem} as found by Damesin et al. (2002), then 12 % of R_{eco} accounted for by R_{stem} in
 464 our study is close to the findings by Janssens et al. (2000).
 465 Upscaling R_{stem} from chamber based measurements to soil surface area for comparison with other
 466 ecosystem respiration components can cause considerable up-scaling biases. Three main causes of
 467 errors can be identified: Insufficient number of measurements in time to catch the temporal
 468 resolution in R_{stem} , insufficient number of measurements to catch the spatial variability in R_{stem}
 469 between and within trees, and uncertainty related to scaling up surface measurements to the entire
 470 surface of the tree stand. The automatic stem chambers ran continuously throughout the year, thus
 471 capturing even the hourly variation of R_{stem} . However, only two stem chambers were available.
 472 Annual R_{stem} between the two were slightly different (264 ± 88 and 191 ± 64 g C m⁻² yr⁻¹)
 473 highlighting the possible variation of R_{stem} for different trees. We did the measurement at a stem
 474 height of 1.3 m. However, it has for some trees been found that stem CO₂ flux can vary with stem
 475 height (Ceschia et al., 2002). This has been found to be caused by various amounts of CO₂

dissolved in the xylem that can diffuse out of the stem and therefore contribute to the apparent CO₂ flux measured by the chamber (Teskey and McGuire, 2002). Some of this CO₂ can be derived from respiration produced elsewhere on the stem, or it can originate from CO₂ produced in the soil that is being dissolved in the soil water, taken up by the roots and transported up through the stem (Aubrey and Teskey, 2009; Bloemen et al., 2013; Teskey and McGuire, 2007). Differences in R_{stem} along the height of the stems could potentially have influenced the annual estimate of R_{stem} , as well as differences in R_{stem} between different trees. This was, however, not tested in the current study.

4.3 Different seasonal contribution of respiration components

We found a strong seasonal pattern in the contributions of R_{soil} and R_{stem} to R_{eco} (Fig. 2). R_{eco} generally followed the variation in temperature throughout the year with highest R_{eco} during the summer growing season. This is usually seen for other temperate forest with growing season during the warm and relatively wet summer (Janssens et al., 2000), in comparison to e.g. Mediterranean ecosystems where R_{eco} is decoupled from temperature during the hot and dry summers, when water becomes a limiting factor (Matteucci et al., 2015).

The variation in the different seasonal contributions of the individual components to R_{eco} have been explained by differences in phenology, and their individual response to temperature (Migliavacca et al., 2015). R_{stem} experienced dramatic differences in the contribution to R_{eco} , with 6 % during winter and 16 % during summer. Although following an overall pattern similar to R_{soil} (Fig. 4), R_{stem} was much lower during winter. The deciduous beech trees shed their leaves during autumn and enter a dormant period until spring. During this period they do not photosynthesize, and transpiration is limited to a minimum (Essiamah and Eschrich, 1986). Thus the transport through the xylem and phloem is limited to a minimum and respiration is limited to only the necessary maintenance respiration (Damesin, 2003). However, during the growing season growth respiration may be a

500 significant part of stem respiration, not directly determined by temperature, but by plant phenology
 501 (Lavigne and Ryan, 1997). The difference in R_{stem} throughout the year may therefore be larger than
 502 what can be expected from a general temperature dependence. Our observation of low R_{stem} , both in
 503 absolute terms and in its contribution to R_{eco} during the winter months, fits well with the pattern of
 504 tree dormancy during winter, and increased growth respiration during summer. Similar seasonal
 505 patterns of R_{stem} have been found in other temperate forests (Acosta et al., 2008; Edwards et al.,
 506 2002; Griffis et al., 2004; Shibistova et al., 2002; Yang et al., 2012, 2014). However, most studies
 507 do not measure R_{stem} during the winter months, making a full comparison difficult.

508 R_{soil} from the manual chambers differed dramatically from R_{stem} by showing a fairly similar
 509 contribution to R_{eco} during both winter, spring and summer of 52, 45 and 49 %, respectively, while
 510 the contribution increased to 79 % during autumn. Unlike the trees, the microorganisms in the soil
 511 do not go into dormancy and can continue to be active and respire, albeit at a slower rate, even
 512 during winter (Beverly and Franklin, 2015). Freezing temperatures, which causes the soil to freeze
 513 and lower R_{soil} dramatically can occur at our site. However, the winter period during this study was
 514 characterized by above-freezing temperatures during daytime for most of the winter; thereby
 515 leaving the entire soil column thawed at most times. The very high contribution of R_{soil} during
 516 autumn coincided with leaf senescence and litterfall. The input of litter to the soil is significant at
 517 the site, and has been found to account for $218 \pm 17 \text{ g C m}^{-2} \text{ yr}^{-1}$ (Wu et al. 2013). Although the rate
 518 of R_{soil} is determined by temperature, the soil organisms will most often respond by increasing R_{soil}
 519 if additional organic matter such as litter is put into the soil (Han et al., 2015). A continuous high
 520 R_{soil} or a peak following litterfall has been found for other temperate forest ecosystems (DeForest et
 521 al., 2009; Hibbard et al., 2005). Thus, it is likely that the input of litter during autumn has kept R_{soil}
 522 at our site high by fuelling heterotrophic respiration. The trees, however, have shed their leaves and
 523 begun to enter dormancy, which lowers the relative contribution of plant respiration to R_{eco} .

524 The automated chamber measurements and the trenching revealed information on the contribution
 525 of autotrophic R_{soil} throughout the year. During summer, R_{soil} of the trenched soil plots was only 51
 526 % of R_{soil} for the intact plots, while it increased to 83 % during autumn, which was comparable to
 527 the pre trenching level of 77 %. This indicated that autotrophic R_{soil} accounted for 49 % during
 528 summer. However, before the trenching in April, R_{soil} of the trenched plots was lower than the intact
 529 soil plots, by only accounted for 77 %, thus indicating heterogeneous undisturbed R_{soil} . Accounting
 530 for this pre trenching difference gives an autotrophic contribution of 34 % during summer.

531 The variation in the seasonal contribution of autotrophic R_{soil} with highest contribution during the
 532 plant growing season was expected and has been observed for several ecosystems (Beverly and
 533 Franklin, 2015; Pumpanen et al., 2015; Hanson et al., 2000). The major reason for the seasonal
 534 pattern of autotrophic R_{soil} is the seasonal pattern of GPP that drives an increase in root respiration
 535 during the growing season (Pumpanen et al., 2015). Hanson et al. (2000) reviewed the contribution
 536 of autotrophic R_{soil} for different ecosystems and found that the contribution of autotrophic
 537 respiration varied from 10 % to more than 90 %, with a mean value for forests of 45.8 %. 50 %
 538 autotrophic R_{soil} was found in a mixed beech spruce forest in the south of Germany (Andersen et al.,
 539 2005). Epron et al., (2001) found a mean autotrophic R_{soil} of 52 %, with highest autotrophic rate of
 540 60 % in July in a French beech forest. Brumme (1995) found that autotrophic respiration comprised
 541 40 % in a central German beech forest. Our trenching was performed in April, making a full
 542 comparison for the entire year impossible. Our estimate of an autotrophic contribution of 34 %
 543 during summer is relatively low compared to prior literature values. However, since the trenching
 544 was only performed a few months prior to the measurements, it is possible that decomposing root
 545 litter from the severed roots may have contributed to the trenched plots, thereby leading to an
 546 overestimated heterotrophic R_{soil} (Díaz-Pinés et al., 2010; Epron et al., 1999; Hanson et al., 2000;

547 Silver et al., 2005; Subke et al., 2006). A second possibility is the presence of deeper living roots
 548 below the trenching depth of 25 cm.

549 Instead of following the variation in GPP, R_{stem} more closely followed R_{soil} and temperature during
 550 spring, summer and autumn (Fig. 4, Fig. 3). Thus the high variation in GPP during the growing
 551 season was not seen for R_{stem} , which could indicate that the magnitude of R_{stem} was independent
 552 from the day to day variations in GPP and the associated high respiration rates that are expected for
 553 the photosynthesizing organs. The dependence on temperature is in line with other studies that have
 554 found a clear temperature dependence of R_{stem} (Harris et al., 2008; Lavigne et al., 1996; Ryan et al.,
 555 1995), although photosynthesis has also been found to partially regulate stem respiration (Zha et al.,
 556 2004).

557

558 **4.4 Diel patterns of respiration**

559 Both R_{stem} and R_{root} showed a clear diel pattern during summer with the highest respiration seen
 560 around 13:00-15:00 CET for R_{stem} , and the highest respiration seen from 9:00-15:00 for R_{root} (Fig.
 561 5o, k). The high R_{stem} during the afternoon is consistent with the findings of other studies (Acosta et
 562 al., 2008; Teskey and Mcguire, 2007; Zha et al., 2004). This distinct diel pattern have been
 563 explained by a temperature response to the diel pattern of temperature (Teskey and Mcguire, 2007).
 564 However, other studies have found diel patterns of R_{stem} different from the diel pattern of
 565 temperature, which has been suggested to be due to the diel pattern of R_{stem} being modified by
 566 photosynthesis and cambium activity independent of temperature (Yang et al., 2014). The diel
 567 pattern of R_{stem} during summer in our study followed the diel pattern of air temperature, thus
 568 suggesting that temperature is a main determining factor for R_{stem} at our site. This is in line with
 569 temperature being the determining factor for R_{stem} at the seasonal scale (Fig. 4, Section 4.3).
 570 However, during winter R_{stem} was very low and showed no diel pattern, which could reflect the tree

571 dormancy during this period (Fig. 5m). The high R_{root} during 9:00-15:00 is consistent with the
 572 findings of other studies that saw highest R_{root} during daytime, which often has been found to be
 573 linked with photosynthesis (Chen et al., 2010; Drake et al., 2008; Lai et al., 2016; Wertin and
 574 Teskey, 2008). During daytime, an increase in R_{root} is seen due to respiration of recently fixed
 575 photosynthates. During nighttime, however, no photosynthesis takes place, leading to the diel
 576 pattern in feeding of photosynthates. Photosynthesis at the DK-Sor site usually peaks at noon,
 577 before the peak in temperature (Pilegaard et al., 2001). This is consistent with the peak in R_{root} in
 578 this study, thus indicating that photosynthates might in part determine the diel pattern of R_{root} during
 579 summer. Interestingly, no diel pattern was seen during winter and autumn (Fig. 5i, l). During
 580 winter, no photosynthesis takes place, and only little photosynthesis takes place in autumn, thus
 581 only a small amount of photosynthates can alter the diel pattern during these periods. During spring,
 582 however, a small peak was seen around 15:00 CET, later than the peak seen during summer (Fig.
 583 5j). Spring was the only season that showed a diel pattern of soil temperature at 5 cm depth (Fig.
 584 6b). Thus, it is possible that the temperature response of R_{root} is dominant during spring.

585 No clear difference in the diel pattern of R_{soil} was seen between the intact and trenched soil plots
 586 (Fig. 5a-h). However, the trenched plots had lower R_{soil} following the trenching, indicating that the
 587 autotrophic contribution to R_{soil} had been completely or partly removed from the trenched plots
 588 (Section 4.3). Heterotrophic R_{soil} has generally been found to respond to temperature on a seasonal
 589 scale, as well as on a diel scale, although a hysteresis on the diel scale between soil temperature and
 590 heterotrophic R_{soil} has also been observed (Chen et al., 2009; Song et al., 2015; Zhang et al., 2015).
 591 In contrast, autotrophic R_{soil} has often been found to be decoupled from temperature on a diel scale,
 592 resulting primarily from substrate transfer to the soil bacteria through carbon exudates from plant
 593 roots (Kuzyakov and Gavrichkova, 2010). Similarly to the increase in R_{root} as a result of increased
 594 levels of fresh photosynthates, the increase in R_{soil} has been found to lag after photosynthesis

595 (Savage et al., 2013; Tang et al., 2005). Whereas we saw an increase in R_{root} during daytime, we did
 596 not see a similar increase in R_{soil} during daytime in the intact soil plot that contained roots. Instead,
 597 a lower daytime R_{soil} was seen for both the intact and trenched soil plots. Soil temperature at 5 cm
 598 depth generally showed no diel pattern for winter, summer and autumn, which would mean no diel
 599 pattern in R_{soil} if only determined by temperature (Fig. 6). It was surprising that no difference was
 600 seen between the intact and trenched soil plots. In a previous study at the site, the diel pattern of
 601 R_{soil} was investigated for intact soil (Brændholt et al. 2017). A similar diel pattern with lower
 602 daytime R_{soil} was observed. However, it was found that the measured soil CO₂ fluxes were
 603 influenced by low atmospheric turbulence, which was found to lead to an overestimation of
 604 measured soil CO₂ fluxes especially during nighttime, which in turn also biased the diel pattern. In
 605 the current study, we removed measurements at low atmospheric turbulence to remove the effect of
 606 overestimation of fluxes, as recommended by Brændholt et al. (2017). It is, however, possible that
 607 overestimation still plays a role. If this effect is larger than the potential differences in the diel
 608 patterns of intact soil and trenched soil, then this effect may overrule the real diel patterns, making
 609 it difficult to make a distinction between the diel patterns.

610

611 5 Conclusions

612 In this study we used the eddy covariance technique together with manual and automated closed-
 613 chambers to quantify the individual components of ecosystem respiration at diel, seasonal and
 614 annual scale. We found that the contribution of R_{stem} to total R_{eco} varied throughout the year, by only
 615 accounting for 6 % of R_{eco} during winter and 16 % during the summer growing season. In contrast,
 616 R_{soil} showed a fairly similar contribution to R_{eco} during winter, spring and summer of 52, 45 and 49
 617 %, respectively, while the contribution increased to 79 % during autumn. We attributed the large
 618 difference in the seasonal contribution of R_{stem} to different phenological stages of dormancy and

619 growth experienced for the trees during the year, whereas we attributed the high contribution of R_{soil}
620 in autumn to the large input of litter from the deciduous beech trees.

621 By the trenching method, we partitioned R_{soil} into its heterotrophic and autotrophic components. We
622 found that autotrophic R_{soil} accounted for 34 % of R_{soil} during summer, a relative low value
623 compared to findings from other studies. However, we could not rule out the possibility that
624 decomposing roots from the trenched soil plots might have led to an overestimated heterotrophic
625 R_{soil} .

626 Diel R_{stem} and R_{root} showed a clear pattern during summer with the highest respiration seen around
627 13:00-15:00 CET for R_{stem} , and the highest respiration seen from 9:00-15:00 for R_{root} . In contrast,
628 R_{soil} showed the lowest respiration during daytime R_{soil} with no clear difference in the diel pattern
629 between the intact and trenched soil plots.

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

635

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639

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893

894

895 **Figure 1:** Annual respiration for the different components of the ecosystem, with the estimated
896 uncertainties shown by error bars. From left to right the bars show: R_{eco} , R_{soil} at the west transect,
897 R_{soil} at the south transect, R_{soil} at the inside fence transect, R_{soil} at the intact soil plots measured by
898 the automated chambers, R_{soil} at the trenched soil plots measured by the automated chambers and
899 R_{stem} . The annual estimated GPP was 2272 ± 136 g C m⁻² yr⁻¹.

900

901

902 **Figure 2:** R_{eco} (total bar height) partitioned into the component respiration rates from R_{soil} (grey)
 903 and R_{stem} (white) on a surface area basis for each month of 2016. The black bars represent the
 904 remaining R_{eco} after R_{soil} and R_{stem} have been subtracted, i.e. from tree branches and leaves. For the
 905 monthly R_{soil} , the average of the manual closed-chamber measurements of the south and west
 906 transect is shown. Note, that for October, R_{eco} was $11.9 \text{ g C m}^{-2} \text{ yr}^{-1}$ lower than the sum of R_{stem} and
 907 R_{soil} .

908

909 **Figure 3:** R_{soil} (solid lines) throughout the year measured by the automated closed-chambers and
 910 soil temperature at 5 cm depth (dashed line). The black solid lines show the R_{soil} for the four plots
 911 with intact soil and the red solid lines show R_{soil} for the two plots with trenched soil. The lines have
 912 been smoothed to show a running five day average.

913

914 **Figure 4:** Mean daily GPP (black line, left y-axis) and R_{stem} (the red lines, right y-axis) throughout
 915 the year. For R_{stem} both plots are shown. The blue dashed line shows the mean daily R_{soil} for the
 916 intact soil plots measured by the automated closed-chambers. R_{soil} have been multiplied with 0.45 to
 917 fit the right respiration scale.

Figure 5: Seasonally averaged diel patterns of R_{soil} for the intact and trenched soil, R_{root} and R_{stem} measured by the automated closed-chambers for each of the four seasons. Error bars show standard deviation. The seasons of winter, spring, summer and autumn are shown in the four columns from left to right, respectively. The four rows from top to bottom show R_{soil} from intact soil, R_{soil} from trenched soil, R_{root} and R_{stem} , respectively. R_{soil} is shown on a soil surface area basis, while R_{root} and R_{stem} are shown on root surface area and stem surface area basis, respectively.

925

926 **Figure 6:** Seasonally averaged diel pattern of soil temperature ($\pm$ standard deviation) at 5 cm depth
 927 measured by soil thermometers installed close to the automated chambers for winter (a), spring (b),
 928 summer (c) and autumn (d).