





Below-canopy contributions to ecosystem CO₂ fluxes in a temperate mixed forest in Switzerland

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1 **Below-canopy contributions to ecosystem CO₂ fluxes in a temperate mixed forest in**
2 **Switzerland**

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11 production

12

13 **Abstract**

14 Forests are structurally complex ecosystems with several canopy layers, each with
15 distinct functional properties contributing differently to the net ecosystem CO₂ exchange. A large
16 number of studies have addressed ecosystem-scale net CO₂ fluxes in forests, but only few studies
17 have investigated the role of the forest understory. The goal of this study was to quantify the
18 below-canopy contribution to ecosystem CO₂ fluxes of a mixed deciduous forest in Switzerland.
19 Below and above-canopy eddy-covariance (EC) measurements were made continuously over two
20 years, complemented by within canopy wind and CO₂ concentration profile measurements.

21 On an annual basis, the below-canopy fluxes indicated a net carbon source dominated by
22 soil respiration, while the above-canopy fluxes were dominated by tree photosynthesis leading to
23 a net carbon sink. Below-canopy fluxes showed a net carbon sink only in spring, with the early
24 emergence of understory plants before overstory canopy leaf-out. Below-canopy respiration
25 partitioned from the EC measurements agreed well with previous chamber-based soil respiration

26 measurements. However, below and above-canopy fluxes became decoupled under full canopy
27 closure, thus leading to unaccounted below-canopy fluxes when measured only above the
28 canopy. Wind and CO₂ concentration profile measurements supported this finding. Decoupling
29 was independent of low turbulence conditions and decoupled periods could be identified using
30 the relationship between the below and above-canopy standard deviation in vertical wind
31 velocity. A decoupling correction was applied to the above-canopy measurements during
32 decoupled periods and corrected annual net ecosystem production (NEP) agreed well with
33 independent estimates from biomass inventory combined with models. Overall, the below-
34 canopy fluxes contributed 79% to annual ecosystem respiration, but only 9% to annual
35 ecosystem photosynthesis. The decoupling correction reduced annual NEP for the site from
36 about 760 to 330 g C m⁻² yr⁻¹. Our results showed that below-canopy EC measurements are
37 essential in this mixed deciduous forest, and likely in many other forests, to fully understand the
38 carbon dynamics within structurally complex ecosystems.

39

40 **1. Introduction**

41 Forests play an important role in the global carbon cycle by sequestering up to 30% of
42 anthropogenic CO₂ emissions (Pan et al., 2011). The magnitude of CO₂ sequestered by a forest
43 varies depending on many factors such as climate, species composition, growth strategy
44 (deciduous or evergreen), stand age and structure (Luyssaert et al., 2007). Forests are structurally
45 complex ecosystems, both vertically and horizontally. In many cases, several layers with distinct
46 functional properties contribute differently to the CO₂ exchange, both in the understory and the
47 overstory (Misson et al., 2007). Although a large number of studies have addressed ecosystem-
48 scale net CO₂ fluxes in forests, only a limited number of studies have investigated the below-

49 canopy contribution, i.e. from understory vegetation and soil, to these ecosystem fluxes
50 (Baldocchi and Vogel, 1996; Baldocchi et al., 1997; Black et al., 1996; Constantin et al., 1999;
51 Falk et al., 2008; Launiainen et al., 2005; Law et al., 2001; Misson et al., 2007).

52 The net CO₂ exchange between a forest and the atmosphere is commonly measured above
53 the canopy using the eddy-covariance (EC) technique (Baldocchi, 2003). Net ecosystem
54 production (NEP) depends on the balance between the amount of CO₂ fixed by gross primary
55 production (GPP) and the amount released through ecosystem respiration (*R*) (i.e., $NEP = GPP - R$).
56 EC measurements of CO₂ fluxes at different heights in forests can be used to separate the flux
57 contribution from below the main canopy to the total ecosystem flux (Misson et al., 2007).

58 Although in some instances such measurements can be problematic due to low wind speed and
59 intermittent turbulence, some studies have shown that subcanopy CO₂ fluxes can be successfully
60 measured after screening out problematic measurements (Baldocchi and Vogel, 1996; Baldocchi
61 et al., 1997; Black et al., 1996; Constantin et al., 1999; Falk et al., 2008; Launiainen et al., 2005;
62 Law et al., 2001; Misson et al., 2007).

63 From the limited number of studies that have thus far investigated the contribution of
64 below-canopy to ecosystem CO₂ fluxes, large variations in below-canopy contributions have
65 been found among sites. While some studies reported that the understory vegetation and soil
66 provided no contribution to stand level NEP fluxes (Rannik et al., 2002), others have shown that
67 even a slight surface moss layer can offset soil respiration losses during days with high
68 irradiance (Janssens et al., 2001). Depending on the leaf area index (LAI) of the overstory, more
69 or less light penetrates through the canopy to the understory vegetation and soil. Most understory
70 species have thus adapted to the low light levels, either by achieving their maximum LAI before
71 canopy leaf emergence, the “phenological escape” (Crawley, 2009; Richardson and O’Keefe,

72 2009), or by reaching a higher quantum yield efficiency at lower irradiance levels (Jones, 2014;
73 Larcher, 2003). The contribution from below-canopy photosynthesis and respiration will
74 therefore depend largely on the specific ecosystem. Understory photosynthesis has been found to
75 contribute between 0 and 39% to total canopy GPP (Misson et al., 2007; Siqueira et al., 2006),
76 while below-canopy respiration represents a larger proportion of the respective total ecosystem
77 respiration flux at 32 to 79% (Law et al., 1999; Misson et al., 2007). The understory vegetation
78 and soil in deciduous broadleaf forests typically contributes more to ecosystem respiration (62%)
79 compared to evergreen coniferous forests (49%) (Misson et al., 2007), often due to differences in
80 understory biomass and/or to the greater amount of nutrients, especially nitrogen, in the
81 decomposing leaves compared to needles (Reich et al., 2003). As the below-canopy contribution
82 depends greatly on specific ecosystems, extrapolation across sites is difficult.

83 Below-canopy EC measurements also have the potential to provide insights on errors in
84 above-canopy EC measurements, particularly due to low turbulence conditions below the forest
85 canopy layer. In some instances, this can help understanding the advection problem, which is
86 present to varying extents at most EC sites. As several studies have indicated thus far, advection
87 is difficult to quantify, even with extensive advection measurement campaigns (Aubinet et al.,
88 2010). A study by Etzold et al. (2010) estimated the influence of advection on the CO₂ flux
89 measured at the Lägeren site in Switzerland during one growing season. Advection accounted for
90 36% of NEP and, as in most other advection studies, filtering low turbulence periods with a u_* -
91 threshold was suggested to compensate for the advective losses of CO₂. Several studies have
92 found additional insights linked to advection for specific sites using below-canopy EC
93 measurements (Burns et al., 2011; Cook et al., 2004; Foken et al., 2012; Jocher et al., 2017;
94 Novick et al., 2014; Staebler and Fitzjarrald, 2004; Thomas et al., 2013; Tota et al., 2008;

95 Vickers et al., 2012; Vickers and Thomas, 2013). Tota et al. (2008) found a significant below-
96 canopy transport of respired CO₂ in an Amazonian tropical rainforest, which was missed when
97 relying only on above-canopy EC measurements, and thus the very large uptake previously
98 reported for the site was incorrect. Jocher et al. (2017) found that the apparent CO₂ uptake
99 measured in winter at a boreal site in northern Sweden was due to the effect of local topography,
100 resulting in a decoupling of the below-canopy air mass from the above-canopy air mass. Thomas
101 et al. (2013) used below-canopy EC measurements to improve the above-canopy NEP estimate
102 of a tall and dense Douglas-fir forest in Oregon, where decoupling below the canopy also led to
103 unrealistically high NEP above the canopy.

104 The overarching goal of this study was to improve the understanding of ecosystem-level
105 CO₂ exchange in a temperate mixed forest in Switzerland using below and above-canopy EC
106 measurements over two years. The specific objectives of this study were to 1) quantify the below
107 and above-canopy CO₂ fluxes, both in terms of photosynthesis and respiration, 2) identify
108 decoupling using the below-canopy fluxes and correct the above-canopy fluxes accordingly, 3)
109 quantify the below-canopy contribution to ecosystem CO₂ exchange, and 4) investigate
110 differences between below-canopy and ecosystem functional responses to environmental drivers.

111

112 **2. Methods**

113 **2.1 Research site**

114 The Lägeren forest site (47°28'42" N, 8°21'52" E, 682 m.a.s.l.) is located on the relatively
115 steep (average 24°) south-facing slope of the Lägeren mountain, northwest of the city of Zurich
116 in Switzerland. The Lägeren temperate mixed forest is characterized by a relatively high species
117 diversity and a complex canopy structure, with European beech (*Fagus sylvatica* L.), ash

118 (*Fraxinus excelsior* L.), European silver fir (*Abies alba* Mill.), sycamore maple (*Acer*
119 *pseudoplatanus* L.), and Norway spruce (*Picea abies* (L.) Karst.) as the dominant species. The
120 mean tree height of dominant trees is 30.6 m (Etzold et al., 2011). The understory vegetation is
121 dominated by wild garlic (*Allium ursinum* L.) of a maximum height of 0.4 m during spring and
122 early summer. The separation between the top of the understory vegetation and the bottom of the
123 overstory canopy is about 15 m. The main soil type is a haplic cambisol, and the forest floor litter
124 layer stays rather thin, as most of it decomposes within a year. The site is part of the Swiss Air
125 Quality Monitoring Network (NABEL) since 1986 and of the Swiss FluxNet since 2004
126 (www.swissfluxnet.ch). Mean annual temperature is 7.4 °C, and mean annual precipitation is
127 1000 mm (Etzold et al., 2011).

128

129 **2.2 Profile measurements**

130 CO₂ and H₂O concentrations were measured using an eight-level profile sampling system,
131 with inlet funnels at 0.1, 1, 3, 5, 9, 27, 44 and 54 m above the ground (Etzold et al., 2010). Intake
132 hoses were connected to a home-built valve switching unit with continuously purged air inlets,
133 consisting of an inner ethylene copolymer coating, an aluminum layer and an outer high-density
134 polyethylene jacket (Synflex™ Type 1300, Johannsen AG, Zurich, Switzerland). Airflow was
135 directed through a small pump inside the valve switching unit to a closed-path IRGA (model LI-
136 7000, LI-COR Inc., Lincoln, NE, USA), so that all eight levels were measured by the same
137 IRGA. The flow through the selection unit during measurements was kept at 1 l min⁻¹ and at 0.4 l
138 min⁻¹ during purging. Switching of the air selection unit and storing of the IRGA analog output
139 (CO₂ concentration, H₂O concentration, cell pressure and temperature) was controlled by a data
140 logger (CR10, Campbell Scientific Inc., Loughborough, UK). Each inlet was consecutively

141 selected for 30 s, and the CO₂ concentration for that inlet was measured during the last 10
142 seconds to avoid contamination among the different levels. Each level was measured every 10
143 minutes, and the measurements were then aggregated to 30 min averages. The reference flow
144 path of the IRGA was consistently scrubbed with ascarite and desiccant (Mg(ClO₄)₂), and a gas
145 of known CO₂ concentration was used to reference the IRGA measurements every three days.

146 In addition to the CO₂ and H₂O vapor profile, vertical profiles of air temperature and
147 relative humidity (Fischer T/F-Sensors, type 431418, K. Fischer GmbH, Drebach, Germany), as
148 well as wind speed and direction (Gill 2-D sonic anemometers, Gill Instruments Ltd.,
149 Lymington, UK) were measured at six heights (1, 5, 9, 27, 44, and 54 m above the ground).
150 Measurements were controlled and stored by a data logger (CR1000, Campbell Scientific Inc.,
151 Loughborough, UK). The measurement interval was 10 sec, and the measurements were then
152 aggregated to 30 min averages.

153

154 **2.3 Eddy-covariance measurements**

155 Continuous turbulent fluxes of CO₂, water vapor and sensible heat were measured below
156 and above the canopy in 2014 and 2015 using the eddy-covariance (EC) technique (Baldocchi,
157 2003). The below-canopy EC system was at a height of 1.5 m above the soil surface, while the
158 above-canopy EC system was at a height of 54 m. The below-canopy EC system was within the
159 main footprint of the above-canopy EC system. The EC instrumentation at each level consisted
160 of an open-path infrared gas analyzer (IRGA) (model LI-7500, LI-COR Inc., Lincoln, NE, USA)
161 and a three-dimensional ultrasonic anemometer-thermometer (models HS (above) and R3
162 (below), Gill Instruments Ltd., Lymington, UK). EC measurements were made at a frequency of
163 20 Hz. Delays were calculated by maximizing the covariance magnitude at high flux.

164 Half-hourly fluxes of CO₂ (F_c , $\mu\text{mol m}^{-2} \text{s}^{-1}$) were calculated from the covariance of
165 vertical velocity and the CO₂ molar density with WPL correction (Webb et al., 1980). As a
166 previous study by Göckede et al. (2008) showed that a conventional two-dimensional coordinate
167 rotation is better suited at this site than a planar fit approach, the coordinate system was aligned
168 with the mean streamlines so that the mean vertical wind vector became zero (Wilczak et al.,
169 2001). Turbulent departures were then calculated by Reynolds averaging of 30-min blocks of
170 data. A half-hourly averaging period was chosen because it is long enough to capture most of the
171 large eddies (i.e., low frequencies) involved in turbulent transport (Finnigan et al., 2003), and
172 stationarity was generally observed for this duration. Frequency response corrections were
173 applied to raw fluxes, accounting for high-pass (Moncrieff et al., 2005) and low-pass filtering
174 (Horst, 1997) (see Figure S 1 in Supplementary Material for below-canopy cospectra). All fluxes
175 were calculated using the *EddyPro* software (v6.1.0, LI-COR Inc., USA).

176 Net ecosystem exchange (NEE) was calculated as the sum of F_c and the rate of change of
177 CO₂ storage in the air column below the height of the EC flux measurements. The rate of change
178 in CO₂ storage in the air column underneath the above-canopy EC measurement level at 54 m
179 was calculated from the mixing ratio measurements of the LI-7000 IRGA sampling the eight
180 profile levels following Morgenstern et al. (2004). When calculating fluxes for the above EC
181 system in relation to the below-canopy system, the rate of change of CO₂ storage was calculated
182 using the profile measurements between the above and below-canopy EC system. Assuming that
183 fluxes of methane and other volatile organic compounds, and drainage of dissolved organic and
184 inorganic C are negligible, NEP was calculated as $-NEE$. Negative NEP values indicate a
185 release of CO₂ to the atmosphere, while positive values indicate CO₂ uptake by the vegetation.
186 NEP, GPP and R with above or below subscripts refer to the respective measurement levels.

187

188 **2.4 Auxiliary measurements**

189 Above-canopy measurements of climatic variables were made at a height of 54 m. Air
190 temperature (T_a) and relative humidity (RH) were measured using a temperature and relative
191 humidity probe (Rotronic MP101A, Bassersdorf, Switzerland) inside a radiation shield. Total
192 incoming direct and diffuse photosynthetic photon flux density (PPFD) was measured using a
193 sunshine sensor (BF2, Delta-T Devices, Cambridge, UK), while reflected PPFD was measured
194 using a quantum sensor (PARlite, Kipp & Zonen B.V., Delft, The Netherlands). Net radiation
195 (R_n) was measured using a CNR 1 four-way net radiometer (Kipp & Zonen B.V., Delft, The
196 Netherlands). The PPFD sensors and CNR 1 were installed pointing south of the tower.

197 Below-canopy measurements of climatic variables were made at a height of 2 m. Total
198 incoming PPFD was measured using a quantum sensor (LI190SB-L, LI-COR Inc., Lincoln, NE,
199 USA). Soil temperature (T_s) and water content (θ) were measured at depths of 5, 10, 20, and 30
200 cm using Decagon ECH₂O EC-20 probes (Pullman, WA, USA). Measurements were controlled
201 and stored by a data logger (CR10X, Campbell Scientific Inc., Loughborough, UK);
202 measurements were made every 30 s and output averaged every 10 min.

203

204 **2.5 Leaf area index and biomass measurements**

205 Overstory leaf area index (LAI) was measured using a LAI-2000 (LI-COR Inc., Lincoln,
206 NE, USA) once a month during the 2015 growing season. The same transect of ten
207 measurements through the forest was repeated consecutively two times to take into account the
208 spatial and temporal variability in canopy cover. The growing season for the deciduous trees at
209 Lägeren is typically from May until October.

210 Understory biomass was also measured once a month during part of the 2014 growing
211 season and during the full 2015 growing season. Understory green (living) biomass was
212 determined by harvesting two 0.20 m x 0.50 m (0.1 m²) ground areas. Plant material was dried
213 for 48 h at 60 °C and weighed. Understory LAI was estimated from the understory biomass
214 measurements based on the relationship for *Allium ursinum* defined in Ernst (1979).

215 NEP from allometric functions (NEP_{biomass}) was calculated using biomass inventories
216 from the Lägeren forest following the approach detailed in Etzold et al. (2011). NEP_{biomass} was
217 estimated as the change in stored carbon in the biomass (boles, branches, twigs, foliage,
218 reproductive organs, coarse and fine roots, and understory vegetation) over time, thereby using
219 allometric relationships for both belowground and aboveground biomass. This approach thus
220 included the net gain of carbon by tree growth and understory production minus the loss by
221 autotrophic and heterotrophic respiration. Regional species-specific equations were used to
222 convert diameter at breast height (DBH) to volume of branches and twigs (Kaufmann, 2001).
223 Species-specific conversion factors for wood density were applied to convert total tree volume
224 into biomass (Assmann, 1986). Pools of foliage and reproductive organs were modelled based on
225 DBH-dependent functions and agreed well with measured litter fall. Coarse root biomass of trees
226 was estimated as a function of DBH, while fine root biomass was estimated as 50% of foliage
227 biomass (de Wit et al., 2006). For more details on these calculations see Etzold et al. (2011).
228 Biomass inventories from 2015 were compared to those from 2005 and 2009 to calculate the
229 mean change in biomass for the forest over these years to give an estimate of the NEP_{biomass} for
230 2015.

231

232 **2.6 Flux analysis and gap filling**

233 **2.6.1 Quality control**

234 Data quality checks were performed daily to ensure that malfunctioning instruments were
235 repaired quickly, thereby ensuring almost continuous data for below and above-canopy EC
236 measurements in 2014 and 2015. The statistical quality of the raw time series was assessed
237 before flux calculations following Vickers and Mahrt (1997). Raw high-frequency data were
238 rejected if (1) spikes accounted for more than 1% of the time series, (2) more than 10% of
239 available data points were statistically different from the overall trend in the half-hour period, (3)
240 raw data values were outside a plausible range, or (4) window dirtiness of the IRGA sensor
241 exceeded 80%. Only raw data that passed all quality tests were used for flux calculations. Half-
242 hourly averaged flux data were rejected if (1) CO₂ fluxes were outside a physically plausible
243 range (-50 to +50 $\mu\text{mol m}^{-2} \text{s}^{-1}$), (2) the steady state test statistic was outside the range $\pm 30\%$, or
244 (3) the integrated turbulence criterion test was outside the $\pm 30\%$ range (Foken et al., 2005).
245 Following the quality tests, 66% (2014) and 70% (2015) of measured data remained for the
246 above-canopy CO₂ fluxes, while 72% (2014 and 2015) of the measured data remained for the
247 below-canopy CO₂ fluxes. Although specific footprint models for below-canopy measurements
248 have yet to be developed, ecosystem-scale footprint models are currently the best available tool
249 to estimate below-canopy footprints (personal communication Natascha Kljun). Based on the
250 footprint model from Kljun et al. 2004, the 90% cumulative footprint area for the below-canopy
251 EC system was estimated to 60 m across slope during daytime and to 200 m at night, while for
252 the above-canopy EC system it was estimated to 200 m across slope during daytime and to 700
253 m across slope during nighttime. The below-canopy flux footprint was always within the
254 footprint of the above-canopy EC system.

255

256 **2.6.2 Partitioning NEP and filling data gaps**

257 Missing values in the measurement time series were gap filled following Barr et al.
258 (2004). NEP was set equal to $GPP - R$. R was estimated as $-NEP$ when GPP was known to be
259 zero, i.e., at night and during the cold periods (periods when both T_a and T_s at 5 cm depth were
260 below $0\text{ }^\circ\text{C}$). The gaps in the R time series were then filled based on the annual logistic
261 relationship between R and T_s as follows,

$$262 \quad R = \frac{r_w(t)r_1}{1 + \exp[r_2(r_3 - T_s)]}, \quad (1)$$

263 where r_1 ($\mu\text{mol m}^{-2} \text{s}^{-1}$), r_2 ($^\circ\text{C}^{-1}$) and r_3 ($^\circ\text{C}$) are model fitted empirical constants. GPP was
264 estimated as $NEP + R$ during daytime or as zero during nighttime and during the cold periods. To
265 fill gaps in GPP data due to gaps in daytime NEP data, a rectangular hyperbolic relationship
266 between GPP and downwelling PPFD was fitted to the GPP data using the equation,

$$267 \quad GPP = \frac{p_w(t)\alpha Q_\downarrow P_x}{\alpha Q_\downarrow + P_x}, \quad (2)$$

268 where α is the initial quantum yield (mol C mol^{-1} photons), Q_\downarrow is the downwelling PPFD (μmol
269 $\text{m}^{-2} \text{s}^{-1}$), and P_x is the photosynthetic capacity ($\mu\text{mol m}^{-2} \text{s}^{-1}$). For both equations, parameters were
270 first obtained for the annual relationships. An additional multiplier, estimated within a 96-point
271 (2-day) moving window, in the numerator of each equation (r_w and p_w) was then allowed to vary
272 over time to account for short-term changes in other environmental variables or phenological
273 stage. The time-varying parameters were determined using a 48-hour moving window moving

274 through the year in increments of 12 hours. Finally, gaps in NEP were filled using the difference
275 between modeled GPP and R .

276

277 **2.6.3 Decoupling assessment**

278 Different stability and turbulence based indices (e.g. Richardson number, turbulent
279 kinetic energy) were tested to determine decoupled periods. However, such indices were
280 unsuccessful at determining decoupled periods, as decoupling at the Lägeren site also occurred
281 under high turbulence, unstable conditions. The coupling of the two layers was therefore
282 assessed using the standard deviation of the vertical wind velocity (σ_w) (e.g. Acevedo et al.,
283 2009). Recent studies have shown that the relationship between σ_w below and above-canopy can
284 be used to describe the coupling of the two layers, as the relationship between the two σ_w is
285 linear when the layers are coupled (Jocher et al., 2017; Thomas et al., 2013). Decoupling was
286 therefore assessed based on the linearity of σ_w below and above the canopy. Below and above-
287 canopy σ_w were found to be coupled during the leafless period of the deciduous trees, and to be
288 decoupled during the leaf-on period of the deciduous trees. In order to determine the onset and
289 end of the decoupled period, a 5-day moving window was used to determine the change in the
290 linearity of the σ_w relationship. As a result of the 5-day moving window, the dates selected have
291 an uncertainty of ± 2 days due to transition times in the phenology of the site. As the decoupled
292 periods were linked to canopy cover, an independent approach using the phenological camera
293 (Stardot Netcam SC5; for more details see Ahrends et al. (2008) and Wingate et al. (2015)) on
294 top of the EC tower and the LAI measurements was also tested to determine decoupled periods.

295

296 **3. Results and Discussion**

297 **3.1 Environmental conditions and phenological development**

298 The observed years 2014 and 2015 showed distinct differences in environmental
299 conditions. The 2014 growing season (mid-May to beginning of October) was cooler and wetter,
300 with a mean air temperature of 14.0 °C and 152 mm of rain, compared to the 2015 growing
301 season that had a mean air temperature of 15.6 °C and 118 mm of rain, in part due to an extended
302 heat wave during the 2015 summer. For both years, the below-canopy PPFD was approximately
303 20% of the above-canopy PPFD before canopy leaf emergence and less than 1% under full
304 canopy closure (Figure 1a). Below-canopy mean air temperatures were consistently warmer than
305 above-canopy, with a difference of on average 2.2 °C during the two years (Figure 1b). Soil
306 temperatures in July-August were on average 2.7 °C warmer in 2015 as compared to 2014 due to
307 the warmer temperatures and reduced soil water content during the 2015 growing season (Figure
308 1c). Soil water content decreased to 10% in July 2015 and remained low for the rest of the
309 summer (Figure 1d) due to the lack of precipitation. Below and above-canopy air temperatures
310 became similar as the dry conditions persisted in 2015, probably due to a reduction in
311 evapotranspiration and an increase in sensible heat flux, common for ecosystems under drought
312 stress (e.g. Teuling et al., 2010; Wolf et al., 2013; Wolf et al., 2016). The prevailing wind
313 directions above the canopy were aligned on slope parallel to the ridge of the Lägeren mountain
314 range in the West to East direction (Figure 2). Below-canopy wind directions followed a similar
315 distribution to the above-canopy wind directions, but with a deflection angle of approximately
316 30° towards the South.

317 The development of overstory and understory leaf area index (LAI) during the 2015
318 growing season at Lägeren differed between the two canopy layers (Figure 3). Overstory LAI

319 increased considerably from April ($2 \text{ m}^2 \text{ m}^{-2}$) to late May ($6 \text{ m}^2 \text{ m}^{-2}$), with the emergence of the
320 deciduous canopy leaves. Understory LAI, predominantly composed of *Allium ursinum*, started
321 growing in March before full canopy leaf-out (second half of April to first half of May), taking
322 advantage of the high light availability in the understory during this period (Figure 1a).
323 Understory LAI, and associated understory biomass, increased until late May and then decreased
324 rapidly as *Allium ursinum* underwent senescence under full canopy closure (Figure 3b).
325 Afterwards, only a few sparse plants of *Hedera helix* L. and *Lamium galeobdolon* (L.) L. s.l.
326 were able to grow in the understory as well as a few seedlings and saplings.

327

328 **3.2 Measured below-canopy CO₂ fluxes**

329 On an annual basis, the below canopy was a strong net source of carbon ($\text{NEP}_{\text{below}} = -647$
330 $\pm 65 \text{ g C m}^{-2} \text{ yr}^{-1}$) (Table 1). Below-canopy carbon losses were larger in 2014 than in 2015
331 (Figure 4a), probably due to limitations on soil respiration due to dry soil conditions in 2015
332 (Figure 1d), as previous studies have shown a reduction in soil respiration at the Lägeren site for
333 soil water content below 15% (Ruehr et al., 2010). Understory vegetation and soil were a net
334 sink of carbon only in spring, with the early emergence of the wild garlic (*Allium ursinum*)
335 before canopy leaf-out (Figure 3), while it was a net source of carbon for the rest of the year,
336 particularly in summer and fall (Figure 4a). Understory GPP (Figure 4b) depended both on
337 weather conditions and tree canopy cover. The phenological escape of understory plants
338 (Crawley, 2009), i.e., when understory plants reach their maximum LAI or photosynthetic rates
339 before overstory canopy closure, was observed during both years in spring (Figure 3). Spring
340 escape is a common adaptation strategy of understory plants, taking advantage of a short-time
341 period with spring warming and high light availability before tree canopy foliage emergence

342 (Crawley, 2009; Mahall and Bormann, 1978; Sparling, 1967), as seen for the wild garlic at the
343 Lägeren site (Figure 3b). During summer 2014, below-canopy GPP was linked to the
344 combination of understory plant species, understory trees, and overstory trees with lower
345 branches below the overstory canopy. In fall, overstory canopy opening only occurred later in
346 October or November when temperatures were colder and the forest floor was covered with a
347 thick layer of dead leaves, thereby inhibiting understory photosynthesis. High respiration rates (\sim
348 $5 \mu\text{mol m}^{-2} \text{s}^{-1}$) in the understory were found in summer at high temperatures with sufficient
349 water availability, and after senescence in fall, when temperatures were high enough ($> 5 \text{ }^\circ\text{C}$) to
350 allow microbial litter decomposition, especially from the nutrient-rich dead deciduous leaves on
351 the soil surface (Figure 4c). During summer and fall 2015, the soil was warmer ($+2.7^\circ\text{C}$ on
352 average) and dryer ($<12\%$) compared to 2014 (Figure 1) due to a long-lasting drought and heat
353 wave. Consequently, soil respiration processes were limited, as can be seen in the reduced
354 below-canopy R for August to November 2015 compared to 2014 (Figure 4c). These reductions
355 measured by the below-canopy EC system are in agreement with those measured in previous
356 years at the site by Ruehr et al. (2010). These dry conditions also led to lower GPP (Figure 4b)
357 and autotrophic respiration below canopy in summer 2015 compared to 2014.

358 Previous studies have found a similar consistent seasonal pattern, as seen in Figure 4c, in
359 the magnitude of soil respiration over the years at Lägeren, ranging from a minimum of about 0.5
360 $\mu\text{mol m}^{-2} \text{s}^{-1}$ in winter to a maximum of about $5.5 \mu\text{mol m}^{-2} \text{s}^{-1}$ in summer (Etzold et al., 2011;
361 Ruehr et al., 2010). The average below-canopy R over the two years ($769 \pm 130 \text{ g C m}^{-2} \text{ yr}^{-1}$)
362 (Table 1) agreed well with the average soil respiration measured by chambers over four years
363 ($890 \pm 46 \text{ g C m}^{-2} \text{ yr}^{-1}$) (Etzold et al., 2011; Ruehr et al., 2010). Lower annual below-canopy R
364 was found in 2015 due to the dry conditions ($639 \text{ g C m}^{-2} \text{ yr}^{-1}$) compared to wetter conditions in

365 2014 ($898 \text{ C m}^{-2} \text{ yr}^{-1}$). As below-canopy R was similar to average soil respiration (Ruehr et al.,
366 2010), this suggested that most of the below-canopy R came from the soil. Overall, despite the
367 possible challenges linked to partitioning below-canopy fluxes, the agreement between the soil
368 respiration measured and below-canopy R showed the feasibility of below-canopy flux
369 partitioning at the Lägeren site. While at some sites common methods for calculating fluxes from
370 below-canopy measurements are impeded by the low turbulence and require different methods
371 (e.g. Jocher et al., 2017), other below-canopy sites also reported suitable turbulence conditions to
372 partition below-canopy EC fluxes based on common methods (Black et al., 1996; Misson et al.,
373 2007).

374

375 **3.3 Measured above-canopy CO₂ fluxes**

376 The above-canopy fluxes were, in comparison to the below-canopy fluxes, a net carbon
377 sink ($\text{NEP}_{\text{above}}$) during most of the year in 2014 and 2015 (Figure 4a). Above-canopy fluxes were
378 a small net source of carbon in winter and transitioned to a net sink in summer. High
379 photosynthesis rates were found in late spring/summer due to favorable light conditions,
380 sufficient water supply and high temperatures, as the deciduous trees gradually started to become
381 active in the second half of May until senescence in October (Figure 3a; Figure 4b). Given that
382 temperatures are high enough, the evergreen trees at the Lägeren site can photosynthesize during
383 most of the year (including winter). This can be seen by the low, but still present, photosynthesis
384 rates in winter (Figure 4b). However, above-canopy respiratory fluxes were unexpectedly low in
385 summer under full canopy cover (Figure 4c). Respiratory fluxes at Lägeren decreased after full
386 canopy leaf-out in the second half of May 2014 and 2015, when they would have been expected
387 to increase due to higher temperatures (higher heterotrophic respiration) and more active biomass

388 respiring (higher autotrophic respiration) (Figure 4c). Respiratory fluxes increased again after
389 leaf senescence in fall. The respiration partitioned from above-canopy measurements was also
390 smaller than that partitioned from the below-canopy measurements during the growing seasons
391 (Figure 4c). Moreover, annual NEP_{above} was on average $758 \pm 10 \text{ g C m}^{-2} \text{ yr}^{-1}$ over the two years
392 (Table 1), which is well outside the range reported for comparable temperate deciduous forests
393 ($311 \pm 38 \text{ g C m}^{-2} \text{ yr}^{-1}$) or evergreen forests ($398 \pm 42 \text{ g C m}^{-2} \text{ yr}^{-1}$) (Luyssaert et al., 2007).
394 Storage fluxes estimated at $3 \text{ g C m}^{-2} \text{ yr}^{-1}$ were found to have only a small influence on annual
395 NEP_{above} . These observations, in combination with the previous study by Etzold et al. (2010),
396 suggested that some fluxes from the below canopy were not accounted for in the above-canopy
397 measurements, which prompted further investigation on a potential decoupling of below and
398 above-canopy fluxes.

399

400 **3.4 Evidence for decoupling**

401 Profile measurements were used to investigate the presence of a decoupling of the below
402 and above-canopy layers, independently of the EC measurements. The profile measurements
403 showed that the largest gradients in CO_2 concentrations throughout the profile occurred during
404 summer (Figure 5a). CO_2 concentration gradients along the 54 m profile were smallest in winter
405 (5 ppm), increased in spring (10 ppm) and reached a maximum in summer (30 ppm) to finally
406 decrease again in fall with canopy leaf senescence (20 ppm). Although higher CO_2
407 concentrations are to be expected near the soil surface in summer due to enhanced soil
408 respiration, these high concentrations were seen only in the lower part of the profile. Only at 9 m
409 height and above were CO_2 concentrations similar to those at the top of the canopy, well mixed
410 with background air as expected (Buchmann et al., 1998; Buchmann et al., 1996). Thus, the high

411 CO₂ concentration layer extended from near the surface to at least 5 m height (but < 9 m). These
412 high CO₂ concentrations moved horizontally with the drainage flow along the surface (as
413 indicated in Figure 2 by the wind directions below the canopy) rather than vertically, particularly
414 during the main growing season. This interpretation is also supported by the within canopy wind
415 speed measurements: wind speed was highest above the canopy, decreased within the canopy
416 layer, but increased again below 10 m towards the surface (Figure 5d), indicating horizontal
417 pressure gradient forces (e.g. Kaimal and Finnigan, 1994) leading to the decoupled below-
418 canopy layer. Similar profiles were found for daytime and nighttime (see supplementary Figure S
419 2).

420 The relationship between the standard deviation of the vertical wind velocity (σ_w) below
421 and above-canopy was also used to investigate for decoupling (Jocher et al., 2017; Thomas et al.,
422 2013). The relationship between σ_w below and above-canopy was more linear, as shown by the
423 higher goodness of fit and less scatter, in spring ($R_{\text{raw}}^2 = 0.40$, $R_{\text{bin}}^2 = 0.76$) and winter ($R_{\text{raw}}^2 = 0.33$,
424 $R_{\text{bin}}^2 = 0.28$) compared to summer ($R_{\text{raw}}^2 = 0.05$, $R_{\text{bin}}^2 = 0.10$) and fall ($R_{\text{raw}}^2 = 0.05$, $R_{\text{bin}}^2 = 0.003$) when
425 no clear relationships could be found due to the large scatter (Figure 6). These results suggested
426 that the two layers at the Lägeren forest were coupled in spring and winter and were decoupled
427 in summer and fall. Interestingly, below-canopy σ_w values during decoupled months tended to
428 be similar or higher than during coupled months (Figure 6). This is unusual given that
429 decoupling is in general found in forests during stable nocturnal periods with low turbulence
430 (e.g. Alekseychik et al., 2013; Belcher et al., 2008; van Gorsel et al., 2011). A 5-day moving
431 window approach was used to identify decoupled periods. Using 5 days of data allowed having
432 enough points to investigate the relationships, while it also considerably reduced the scatter

433 shown for the seasons in Figure 6, with greater goodness of fit for coupled periods ($R_{\text{raw}}^2 = 0.76$,
434 $R_{\text{bin}}^2 = 0.93$) compared to decoupled periods ($R_{\text{raw}}^2 = 0.17$, $R_{\text{bin}}^2 = 0.32$) (Figure 7). Based on the 5-
435 day moving window approach, the decoupled periods during the two years of measurements
436 were from June 1 to October 14 in 2014 and from May 20 to October 14 in 2015 (± 2 days for all
437 dates). These decoupled periods corresponded to periods with full canopy cover, as determined
438 using the phenological camera on top of the EC tower and the LAI measurements, from June 1 to
439 October 15 in 2014, and from May 20 to October 15 in 2015. The onset of these periods
440 coincided with a sharp and constant reduction in above-canopy R (spring), while an increase in
441 above-canopy R (fall) indicated the end of the decoupled period. It is important to note that
442 decoupling does not stop when above-canopy photosynthesis declines, but rather when the leaves
443 have fallen, which can be more than a month after the above-canopy deciduous leaves have
444 become senescent.

445 During the decoupled periods, the mean directional wind shear between below and
446 above-canopy was also found to increase past the 70° threshold (see supplementary Figure S 3).
447 Although in some studies wind shear can be directly linked to decoupling (e.g. Alekseychik et
448 al., 2013), the wind shear was not consistently linked to decoupling at the Lägeren site (see
449 supplementary Figure S 3). Several studies have associated decoupling to stable conditions (e.g.
450 Alekseychik et al., 2013; van Gorsel et al., 2011). However, after testing with turbulent kinetic
451 energy (see supplementary Figure S 4) and with Richardson numbers (see supplementary Figure
452 S 5), it was found that decoupling at the Lägeren site could not be defined based on stability
453 based indices as it also occurred during unstable, turbulent daytime conditions.

454

455 **3.5 Decoupling and advection at the Lägeren site**

456 Etzold et al. (2010) estimated the influence of advection for the ecosystem CO₂ flux
457 measured at the Lägeren site to be 36% for the period from May to August 2007 using a two-
458 dimensional approach along the slope with profile measurements. They estimated that the forest
459 fixed 157 g C m⁻² less than what the direct EC measurements above the canopy suggested for
460 these four months. Several studies have shown that the filtering of low turbulence periods (low
461 u_*) results in a systematic decrease in annual NEP, which can range from 50 to 200 g C m⁻² yr⁻¹
462 (Carrara et al., 2003; Falge et al., 2001; Hui et al., 2004; Papale et al., 2006). Following this line
463 of argumentation, a u_* -threshold of 0.30 m s⁻¹ was suggested by Etzold et al. (2010) to account
464 for periods with advection at this site, leading to an increase in respiration of 107 g C m⁻² and
465 consequently, to a decrease in NEP by the same amount. Although filtering with a u_* -threshold is
466 often used as the best practice to deal with advection, it only accounted for 2/3 of the advection
467 flux empirically estimated from horizontal and vertical gradient measurements during the four
468 months of direct comparison by Etzold et al. (2010).

469 In this study, u_* -filtering was not used to enable a detailed investigation of the measured
470 contributions of below and above-canopy fluxes, and also because the decoupling was not
471 confined to periods of low turbulence at night. In addition, the common methods for determining
472 the u_* -threshold (e.g. Goulden et al., 1997; Gu et al., 2005) cannot be used at the Lägeren site as
473 they do not detect a threshold, i.e., there is no inflection point. Instead, the integral turbulence
474 criterion test (Foken et al., 2005) and other quality filtering (see Section 2.6.1) were used to
475 ensure of the quality of the fluxes. Above-canopy u_* -values were relatively high for both years at
476 Lägeren, with most values being in the range of 0.40-0.45 m s⁻¹ during nighttime and in the range

477 of 0.45-0.60 m s⁻¹ during daytime, indicating good turbulent mixing even at night. The
478 discrepancy therefore seemed to lie in the fluxes actually reaching the EC system above canopy
479 and not primarily in low turbulence conditions *per se*.

480 The below-canopy EC measurements at Lägeren provided crucial additional insights to
481 better understand these carbon dynamics and a potential decoupling of below and above-canopy
482 fluxes. The uncommonly large measured annual NEP_{above} and the reduction in R_{above} during the
483 growing season, as well as the additional investigations they prompted, indicated that starting
484 with full canopy closure in the second half of May/beginning of June, a decoupling between
485 below and above-canopy fluxes occurred (Figure 4c). As the annual below-canopy fluxes at
486 Lägeren are dominated by respiration (except during spring), this led to an overestimation of
487 annual ecosystem NEP ($758 \pm 10 \text{ g C m}^{-2} \text{ yr}^{-1}$) and a large underestimation of ecosystem R (494
488 $\pm 5 \text{ g C m}^{-2} \text{ yr}^{-1}$), while GPP was only slightly affected ($1252 \pm 5 \text{ g C m}^{-2} \text{ yr}^{-1}$) (Figure 4 and
489 Table 1). The decoupling influence was also greater in 2014 than in 2015 due to the greater
490 influence of soil respiration (Figure 4c and Table 1).

491 Below-canopy air masses in a forest can be affected by the local topography, thus
492 resulting in a horizontal exchange along the surface (Belcher et al., 2008; Belcher et al., 2012).
493 Decoupling is therefore often associated with nighttime conditions, as turbulence within the
494 canopy collapses under stable stratification, while the flow above canopy remains turbulent
495 (Belcher et al., 2008). The air within the canopy then creates downslope drainage currents,
496 thereby not reaching the EC measurements above canopy (Aubinet et al., 2005; Belcher et al.,
497 2008; Feigenwinter et al., 2004; Staebler and Fitzjarrald, 2004). Despite the predominance of
498 decoupling during nighttime at most sites (e.g. Alekseychik et al., 2013; van Gorsel et al., 2011),
499 some sites are also affected by decoupling during daytime due to the influence of local

500 topography (Jocher et al., 2017) or of a dense canopy cover (Thomas et al., 2013). At the
501 Lägeren site, the tree canopies created a mechanical barrier, which led to decoupled flow layers
502 below and above this barrier; the scalars (e.g. CO₂) that remain in the below-canopy layer could
503 then be advected away. Consequently, the below-canopy fluxes were not fully measured by the
504 above-canopy EC system in 2014 and 2015. Under decoupled conditions, NEP based on above-
505 canopy measurements does not reflect the entire ecosystem, but rather the upper layer, i.e., the
506 tree canopies. As a result, decoupling often results in a considerable overestimation of above-
507 canopy NEP, as below-canopy fluxes, which are dominated by *R*, are advected away from the
508 ecosystem without being measured (Goulden et al., 1996; Thomas et al., 2013).

509

510 **3.6 Correcting above-canopy CO₂ fluxes for decoupling**

511 Thomas et al. (2013) suggested a correction for decoupled subcanopies that consisted of
512 adding the below-canopy fluxes, which in their study were only composed of soil respiration
513 (i.e., no understory vegetation), to the above-canopy fluxes during decoupled periods. The
514 subcanopy correction decreased the unrealistically high NEP_{above} of 1100 g C m⁻² yr⁻¹ for their
515 forest in Oregon to a more realistic 480 g C m⁻² yr⁻¹. At Lägeren, the decoupling was observed
516 under full canopy closure, i.e. when all deciduous leaves were out, and thus, the missing above-
517 canopy fluxes were recovered using the decoupling correction approach from Thomas et al.
518 (2013) during the identified decoupled periods. As some understory plants are present at the
519 Lägeren site, this decoupling correction implied adding the net fluxes from the below canopy,
520 composed of both below-canopy *R* and understory GPP, to the above-canopy fluxes when the
521 measurements from the two layers were decoupled. As the decoupling and associated drainage
522 flow at the Lägeren site occurs within the lower 9 m of the tree trunks (Figure 5), it could

523 therefore be assumed that R and GPP occurring within the tree canopy remained unaffected by
524 the drainage flow and were accurately measured by the above-canopy EC system.

525 The decoupling correction resulted in a large increase in R_{above} and associated decrease in
526 NEP_{above} , while GPP_{above} was only slightly increased (Figure 8). Following the correction, R_{above}
527 increased during the growing season, as would be expected with the higher temperatures and
528 greater biomass respiring (Figure 8c). R_{above} followed similar trends as R_{below} , being on average 1
529 to 2 $\mu\text{mol m}^{-2} \text{s}^{-1}$ greater. R_{above} reached a maximum of about 7 $\mu\text{mol m}^{-2} \text{s}^{-1}$ in July-August, when
530 R_{below} also reached a maximum of about 5 $\mu\text{mol m}^{-2} \text{s}^{-1}$. A secondary maximum in both R_{above} and
531 R_{below} was observed in 2014 due to the decomposition of dead deciduous leaves on the soil
532 surface (Figure 8c), as temperature and soil water content were not limiting (Figure 1). However,
533 this secondary maximum in R was not seen in 2015 due to low soil water content (~12%) which
534 lasted until November 2015 (Figure 1d). In addition, the decoupling correction also led to a small
535 increase of 3% in energy balance closure when added to the sensible and latent heat fluxes (see
536 supplementary Figure S 6).

537

538 **3.7 Comparison of functional relationships for uncorrected and corrected fluxes**

539 Uncorrected above-canopy respiration increased with soil temperature, but levelled off at
540 about 2 $\mu\text{mol m}^{-2} \text{s}^{-1}$ (Table 2) when soil temperatures were 5-6 °C in 2014 and 2015 (Figure 9).
541 In contrast, below-canopy respiration increased exponentially with temperature until respiration
542 reached about 4 $\mu\text{mol m}^{-2} \text{s}^{-1}$ at 12°C in 2014 and 14 °C in 2015, before levelling off (Figure 9)
543 when soil water content became limiting. This interpretation is supported by the fact that during
544 the entire year, the below-canopy respiration was mostly coming from the soil (Etzold et al.,
545 2011; Ruehr et al., 2010) and thus, it was strongly affected by temperature, soil volumetric water

546 content (summer) and substrate availability (e.g., dead leaves in fall) (Figure 4c). Applying the
547 decoupling correction allowed recovery of the below-canopy R that was missing from above-
548 canopy R and sharply increased the goodness of fit as well (Table 2). After the correction, above-
549 canopy R increased exponentially with temperature, reflecting both the effect of increasing
550 autotrophic respiration from the living biomass and heterotrophic respiration from decomposition
551 (Figure 9).

552 Compared to R , the effect of the decoupling correction on GPP was much smaller, as the
553 annual below-canopy fluxes were dominated by respiration, except for a short period in
554 spring/early summer (Figure 4). GPP did not change substantially following the correction
555 (Figure 10), especially in 2015 when below-canopy GPP was very low with $57 \text{ g C m}^{-2} \text{ yr}^{-1}$
556 compared to $187 \text{ g C m}^{-2} \text{ yr}^{-1}$ in 2014 (Table 1). This was also shown by very similar quantum
557 yields as well as R^2 values, although slightly lower due to the inclusion of understory vegetation,
558 for corrected vs. uncorrected above-canopy GPP data (Table 3). Below-canopy GPP was
559 constrained by PPFD in 2014 as there was still GPP during the summer under low light
560 conditions, while in 2015 below-canopy GPP was mostly during the high light conditions in
561 spring (Figure 4b). Consequently, the understory vegetation showed a typical hyperbolic
562 relationship with PPFD in 2014, saturating at about $2 \mu\text{mol m}^{-2} \text{ s}^{-1}$ (Table 3), but did not saturate
563 as much in 2015.

564

565 **3.8 Implications for carbon budget at the Lägeren site**

566 Adding the below-canopy fluxes to the above-canopy fluxes led to a decrease in overall
567 carbon uptake (NEP) from the site. The decoupling correction reduced the average annual
568 $\text{NEP}_{\text{above}}$ from $758 \pm 10 \text{ g C m}^{-2} \text{ yr}^{-1}$ to $327 \pm 4 \text{ g C m}^{-2} \text{ yr}^{-1}$, mostly by increasing R (see Table 1).

569 After leaf emergence, below and above-canopy NEP distinctly diverged because of CO₂
570 assimilation by the overstory while below-canopy respiration increased (Figure 8), similar to
571 what was found previously in deciduous forests (Black et al., 1996). Positive above-canopy NEP
572 showed the carbon uptake of the system as a whole, while negative below-canopy NEP showed
573 the release of carbon. In the synthesis study by Misson et al. (2007), eight of the eleven below-
574 canopy sites studied were also sources of carbon during summer. The correction of the above-
575 canopy fluxes during the decoupled period led to an increase in R_{above} of 50% in 2014 and of
576 48% in 2015 (Table 1). Overall, GPP_{below} contributed only 9% to GPP_{above} , while R_{below}
577 contributed 79% to R_{above} (Table 1). These average relative flux contributions from the Lägeren
578 below-canopy layer were within the ranges reported from previous studies, with 0 to 39% for
579 GPP and 32 to 79% for R (Misson et al., 2007). The contribution from GPP_{below} at Lägeren was
580 lower than the average of 14% found by Misson et al. (2007), probably because Lägeren is a
581 dense forest with a relatively high LAI, while the contribution from R_{below} was above the average
582 of 55%.

583 Moreover, following the decoupling correction, NEP_{above} agreed well with NEP estimates
584 derived from allometric functions using biomass inventory data combined with models for
585 respiration ($NEP_{\text{biomass}} = 331 \pm 10 \text{ g C m}^{-2} \text{ yr}^{-1}$). In a previous study by Etzold et al. (2011),
586 NEP_{biomass} was estimated at $307 \text{ g C m}^{-2} \text{ yr}^{-1}$ (296 to $319 \text{ g C m}^{-2} \text{ yr}^{-1}$) based on data from 2005 and
587 2009. Biomass inventory data from 2015 indicated that trees grew on average 8% since 2005 and
588 5% since 2009, leading to a NEP_{biomass} from allometric functions of 321 to $341 \text{ g C m}^{-2} \text{ yr}^{-1}$. These
589 results therefore suggest that the decoupling correction was effective in recovering the part of the
590 flux which was not measured above-canopy and led to NEP values close to independent NEP
591 estimates for the site as well as to other temperate deciduous forests comparable to Lägeren

592 (Luyssaert et al., 2007). Indeed, average annual NEP ($327 \pm 4 \text{ g C m}^{-2} \text{ yr}^{-1}$), GPP ($1297 \pm 28 \text{ g C}$
593 $\text{m}^{-2} \text{ yr}^{-1}$) and R ($970 \pm 25 \text{ g C m}^{-2} \text{ yr}^{-1}$) at Lägeren in 2014 and 2015, were well within the ranges
594 recorded for similar temperate deciduous forests for NEP ($311 \pm 38 \text{ g C m}^{-2} \text{ yr}^{-1}$), GPP ($1375 \pm$
595 $56 \text{ g C m}^{-2} \text{ yr}^{-1}$) and R ($1048 \pm 64 \text{ g C m}^{-2} \text{ yr}^{-1}$) (Figure 11).

596 In comparison, although the approach from Etzold et al. (2010) helped in reducing the
597 annual NEP in 2014 and 2015, NEP was still higher than our corrected NEP estimates with $536 \pm$
598 $35 \text{ g C m}^{-2} \text{ yr}^{-1}$ when using the u_* -filtering and with $484 \pm 7 \text{ g C m}^{-2} \text{ yr}^{-1}$ when removing 36%
599 advection (Table 4). Moreover, u_* -filtering did not fully resolve the decoupling problem (see
600 supplementary Figure S 7), as it is only applied to low turbulence conditions at night whereas
601 decoupling also occurred under turbulent conditions, while the 36% advection correction can
602 only be applied to annual sums and cannot correct the high-resolution flux time series available.
603 Other studies have also shown that the u_* -threshold can be insufficient in accounting for
604 advection or is not necessarily a good indicator for below-canopy turbulence (Jocher et al., 2017;
605 Speckman et al., 2015; van Gorsel et al., 2011).

606 Although the goal of the decoupling correction was to obtain more reliable net CO_2
607 exchange estimates, it should be noted that the correction bears the risk of double accounting if
608 some eddies would eventually reach the above-canopy EC system. However, these net ecosystem
609 carbon budgets are the best available direct estimates of the ecosystem CO_2 exchange, given the
610 challenging measurement conditions for complex forest sites such as Lägeren. For our site, the
611 decoupling correction reduced the high NEP estimates to a range closer to biomass-derived NEP
612 for the site, indicating a successful accounting for the decoupling. Although the uncertainties in
613 the corrected NEP estimates are difficult to quantify, such uncertainties are inherent to sites with

614 considerable advection (Kutsch et al., 2008) given the complexity of the problem and that even
615 with extensive advection measurements, it is difficult to fully quantify its magnitude (Aubinet et
616 al., 2010).

617

618 **3.9 Importance of below-canopy measurements**

619 Decoupling is present to varying extents at diverse EC sites and its effect on measured net
620 ecosystem carbon budget is often unknown until additional measurements are performed. Below-
621 canopy EC measurements can provide unique insights on below-canopy carbon dynamics and
622 turbulence, which are often lacking when relying only on above-canopy EC measurements and
623 thereby, can help improve the accuracy of forest carbon budgets. In extreme cases, below-canopy
624 measurements can enable realistic NEP estimates for forests known to be completely decoupled
625 due to dense canopy covers (Thomas et al., 2013). In some cases, below-canopy measurements
626 will help resolve inconsistencies such as winter uptake in measured above-canopy fluxes (e.g.
627 Jocher et al., 2017). In many other cases, such as Tota et al. (2008) and this study, below-canopy
628 measurements will complement the above-canopy measurements in a way that could not have
629 been predicted otherwise and allow a more accurate NEP estimation for the site. It is however
630 important to note that below-canopy fluxes can unfortunately not be derived at all sites due to the
631 low turbulence conditions making the EC flux calculations impossible. However, even in such
632 cases, alternative methods such as the conditional sampling method (Desjardins, 1977; Thomas
633 et al., 2008) can be used to estimate the flux. The common practice in the flux community to
634 account for decoupling or advection by filtering based on above-canopy u_* -threshold has been
635 shown to be ineffective at many sites (e.g. Acevedo et al., 2009; Jocher et al., 2017; Speckman et

636 al., 2015; van Gorsel et al., 2011) and below-canopy measurements can offer the solution needed
637 at some of these sites.

638

639 **4. Conclusions**

640 Concurrent below and above-canopy EC measurements captured the very different
641 carbon dynamics of the respective layers well: while the above canopy was a net carbon sink, the
642 below canopy was a net source during most of the year, except in spring. Below and above-
643 canopy fluxes were decoupled during the growing season, resulting in a large overestimation of
644 the measured net ecosystem-scale carbon uptake for this mixed forest site. The measurements of
645 below-canopy fluxes enabled the correction of this overestimation, and corrected ecosystem
646 fluxes agreed well with independently estimated NEP from biomass inventories combined with
647 models. Our results clearly demonstrated that below-canopy EC measurements are essential in
648 this mixed forest, and likely in many other forests, to gain reliable estimates of the CO₂ exchange
649 in structurally complex forest ecosystems.

650

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661

662

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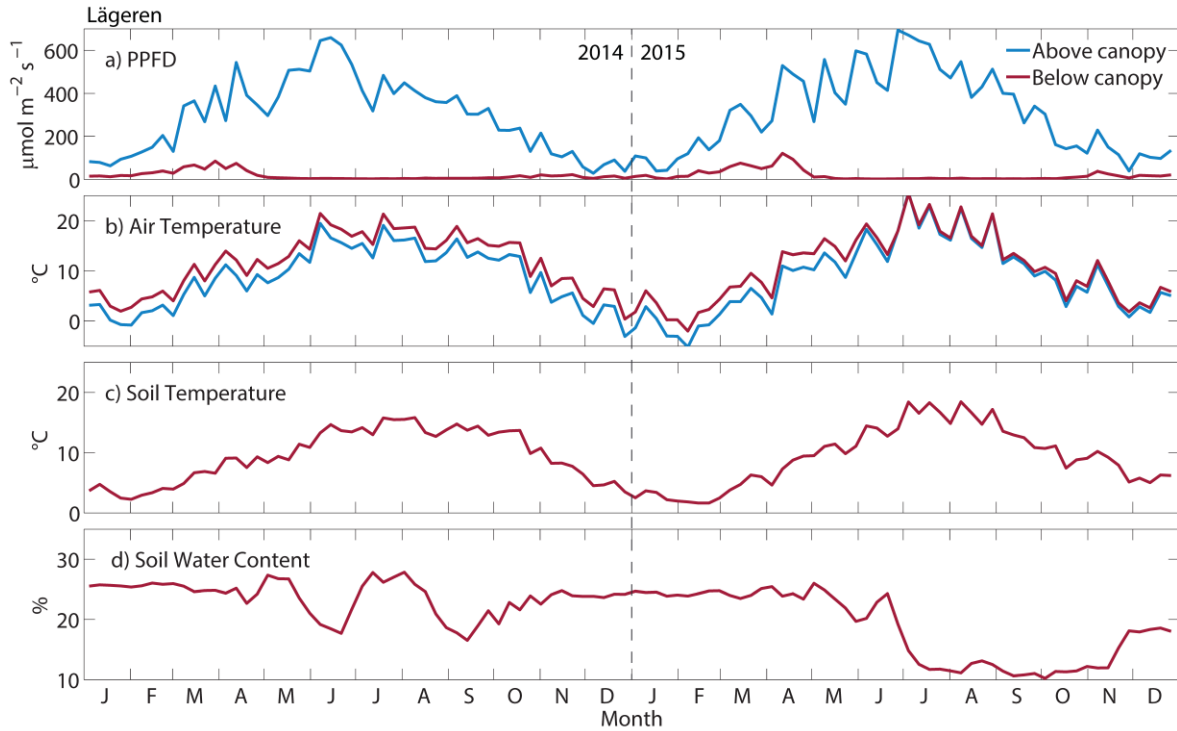
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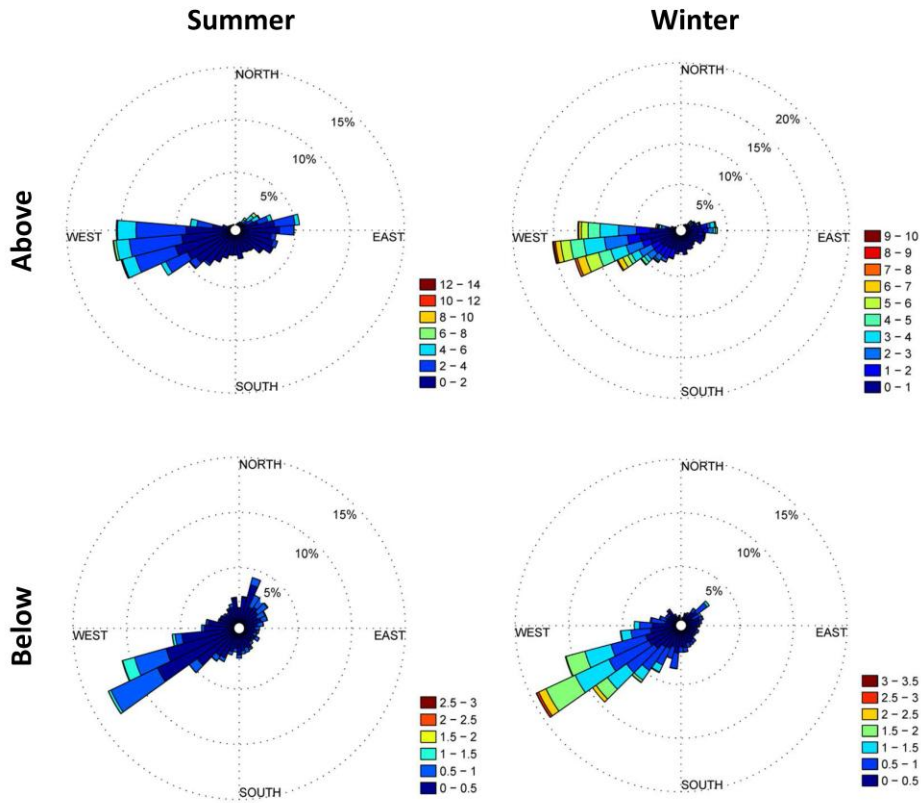
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881 **Figures**
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884 **Figure 1:** Climatic variables for a) photosynthetic photon flux density (PPFD), b) air temperature, c) soil
885 temperature and d) soil water content at Lägeren in 2014 and 2015. The blue lines represent above-canopy
886 measurements, while the red lines represent below-canopy measurements. Air temperature above canopy was
887 measured at 54 m height and below canopy at 2 m height. Soil temperature was measured at 5 cm depth and the soil
888 water content at 10 cm depth. All lines are 5-day averages.
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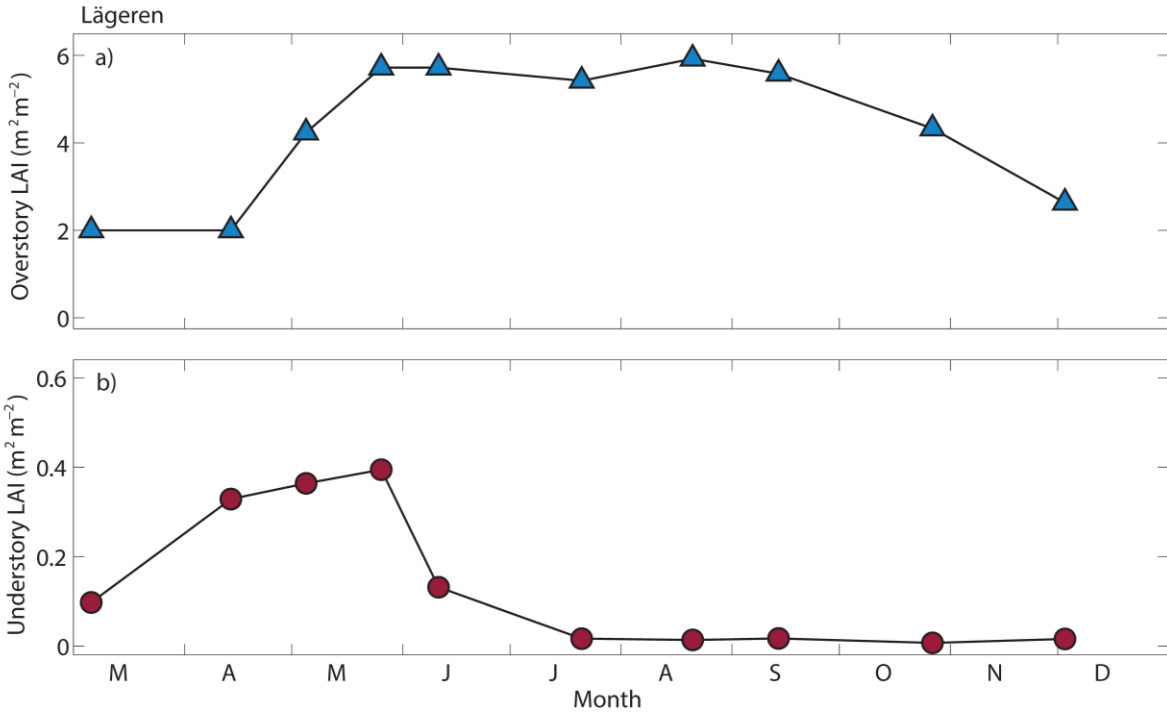
890
 891 **Figure 2:** Distribution of wind directions (%) and respective wind speeds (m s^{-1}) in 2014 at Lägeren for above (54
 892 m) and below (2 m) canopy in summer and winter. Seasons are defined based on the meteorological definition for
 893 summer (JJA) and winter (DJF). A similar wind distribution was found in 2015. Please note the different scaling
 894 between seasons.
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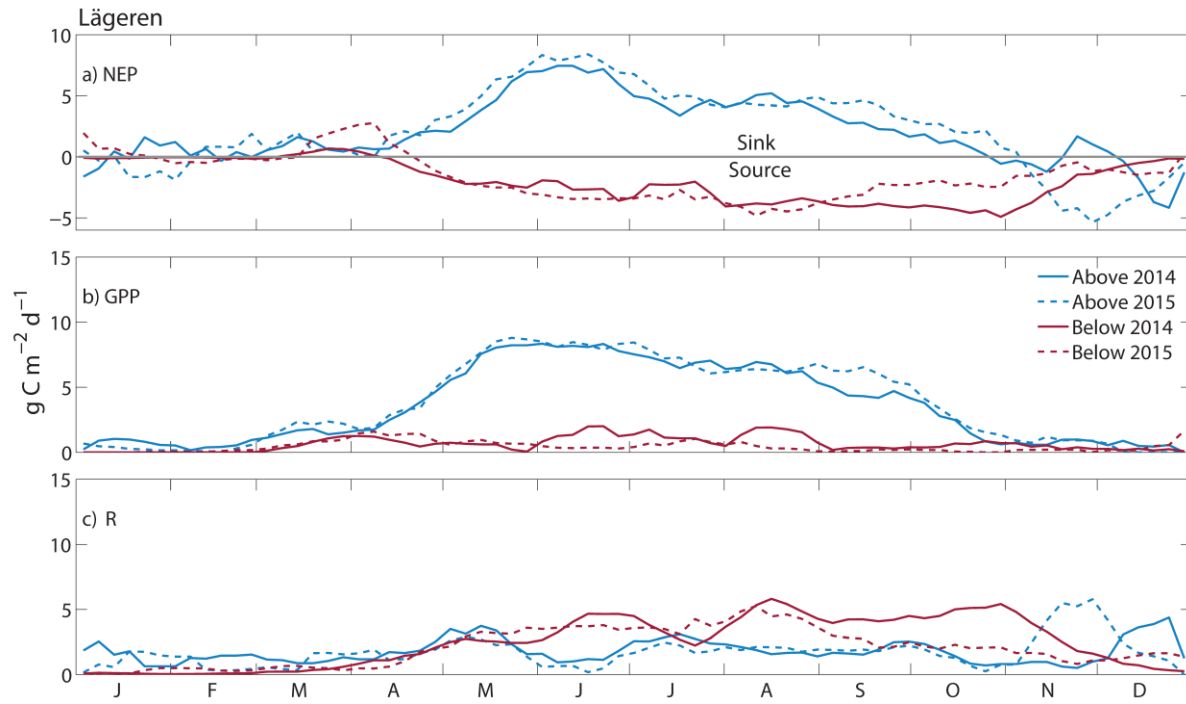


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901 **Figure 3:** Overstory and understory LAI during the 2015 growing season at Lägeren. The blue triangles in a)
 902 represent the average of two transects of ten LAI measurements and the red circles in b) represent LAI estimated
 903 following Ernst (1979) from the biomass measurements. Please note the factor of 10 difference in y-axis scaling
 904 between panel a) and b).

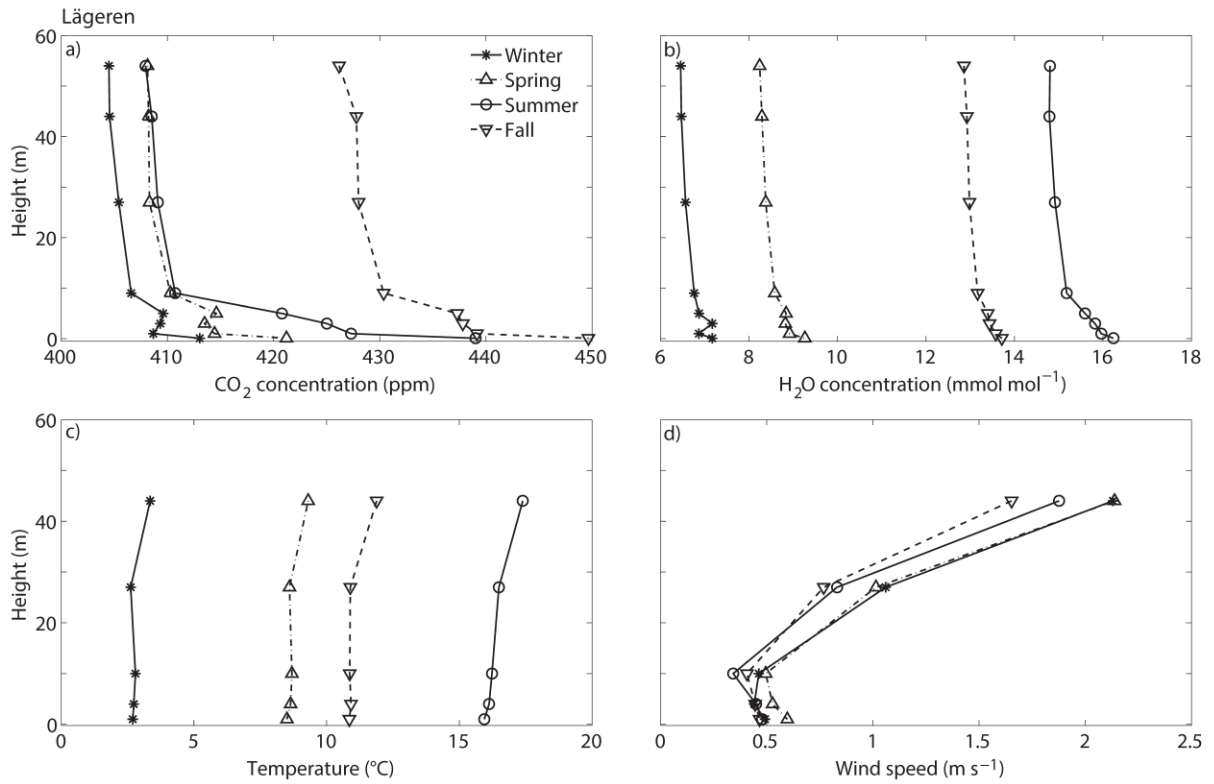
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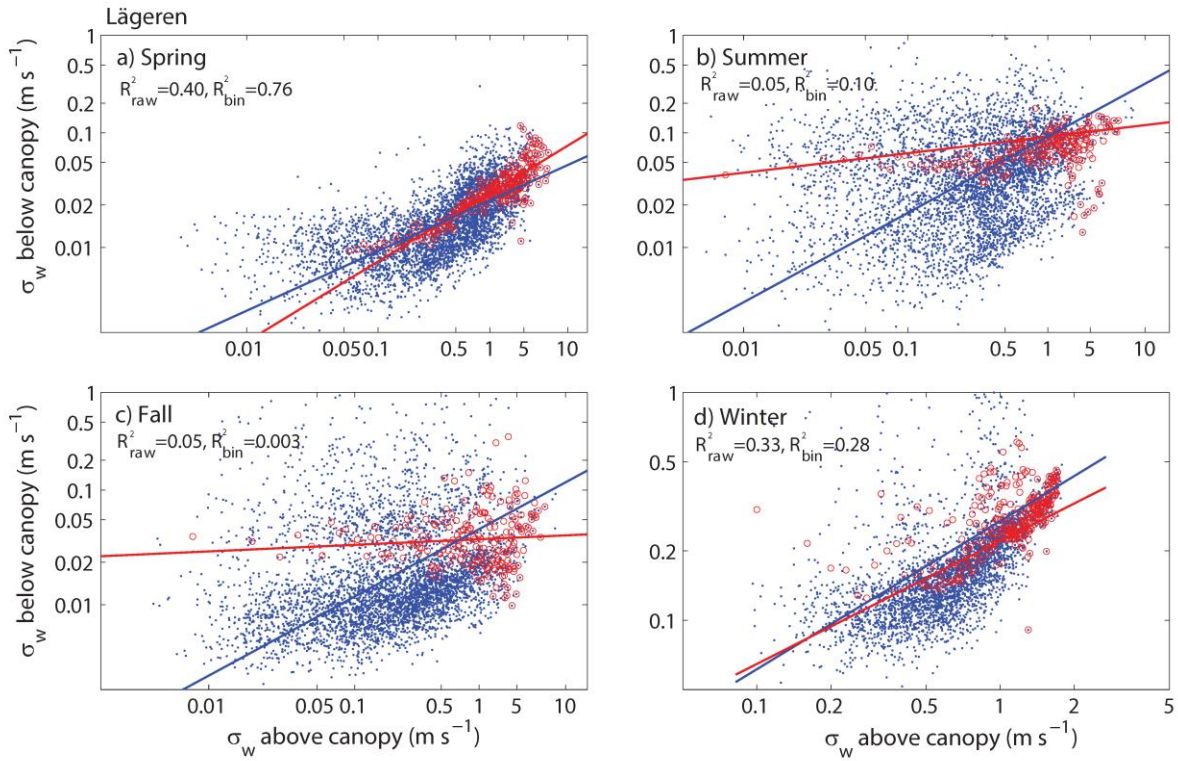
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908 **Figure 4:** Measured net ecosystem production (NEP, panel a), gross primary production (GPP, panel b) and
 909 respiration (R , panel c) above and below the canopy (without decoupling correction) at Lägeren in 2014 and 2015.
 910 All lines are 5-day averages.
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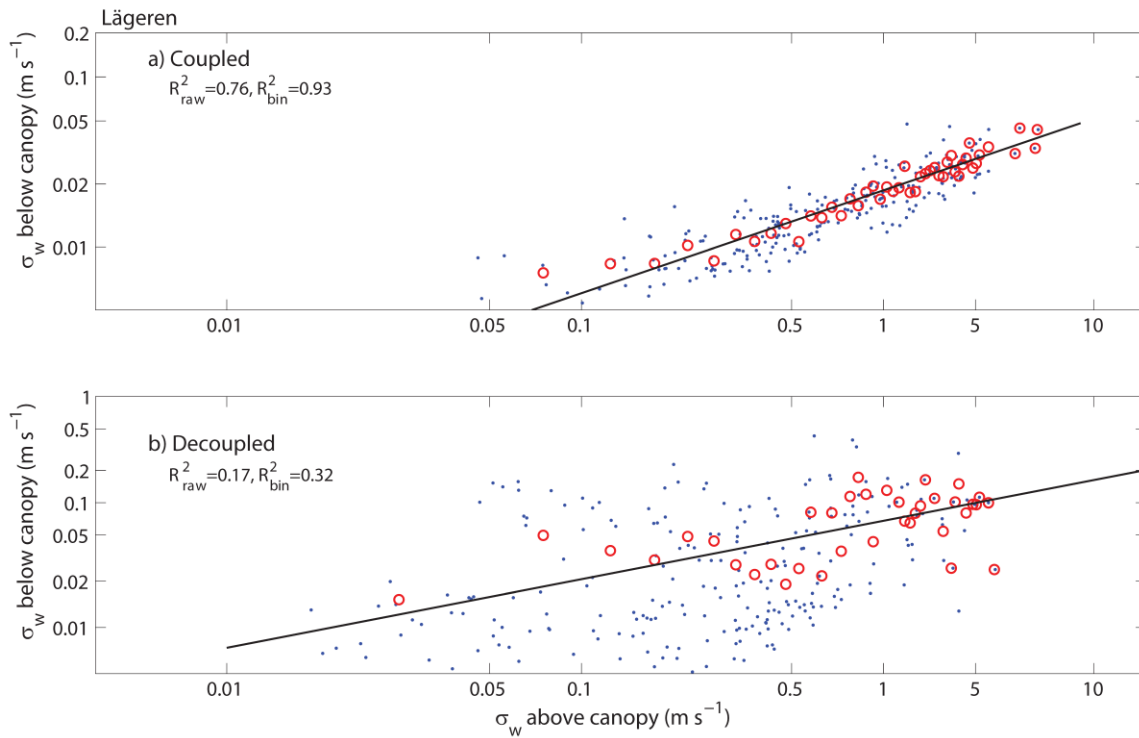
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Figure 5: Seasonal profiles of mean a) CO₂ concentration, b) H₂O vapor concentration, c) temperature and d) wind speed within the canopy at Lägeren in 2014. Seasons are defined based on the meteorological definition for winter (DJF), spring (MAM), summer (JJA) and fall (SON). The average tree canopy height is 30 m, with the average tree canopy crown extending from 25 to 35 m. See supplementary Figure S 2 for daytime and nighttime profiles.



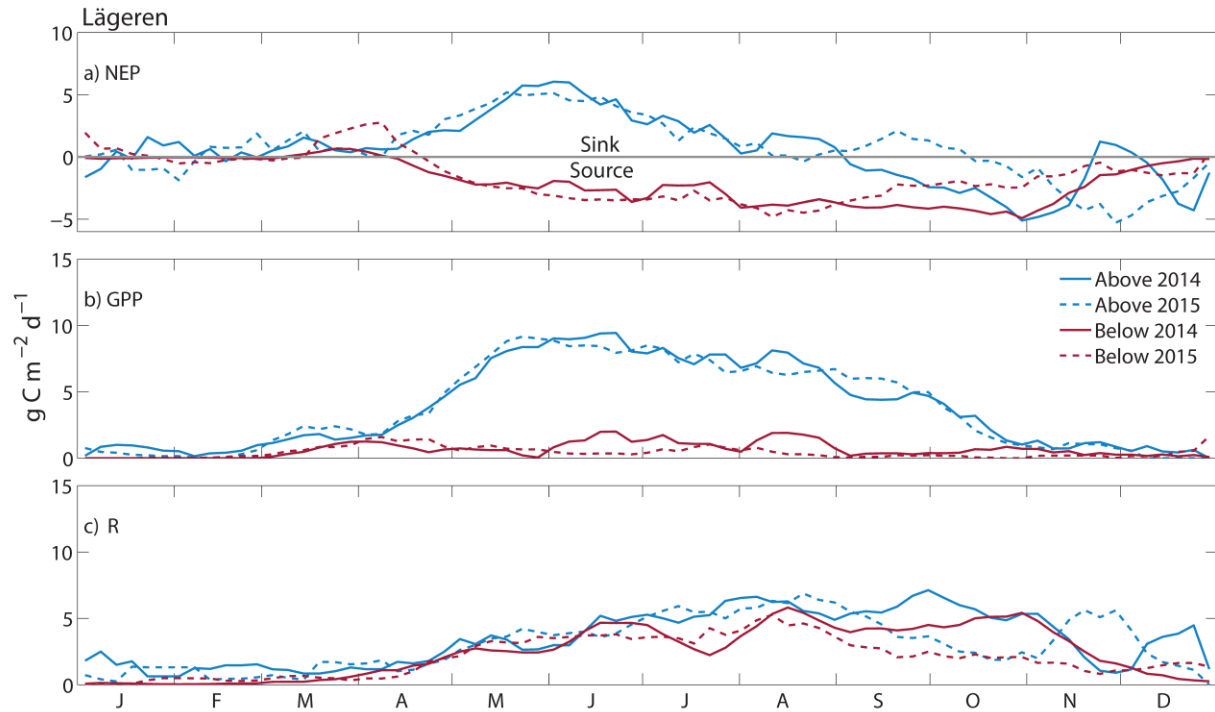
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Figure 6: Relationships between standard deviations in vertical velocity (σ_w) below and above canopy for a) spring, b) summer, c) fall and d) winter in 2014. Seasons are defined based on the meteorological definition for winter (DJF), spring (MAM), summer (JJA) and fall (SON). The blue dots represent the half-hourly measurements over the 5 days and the red circles are binned by 0.05 m s^{-1} .



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Figure 7: Standard deviation in vertical wind velocity (σ_w) for below and above canopy for the 5-day moving window showing an example for the a) coupled condition (May 10 to 15 2014) and b) decoupled condition (June 9 to 14 2014). The blue dots represent the half-hourly measurements over the five days and the red circles are binned by 0.05 m s^{-1} .

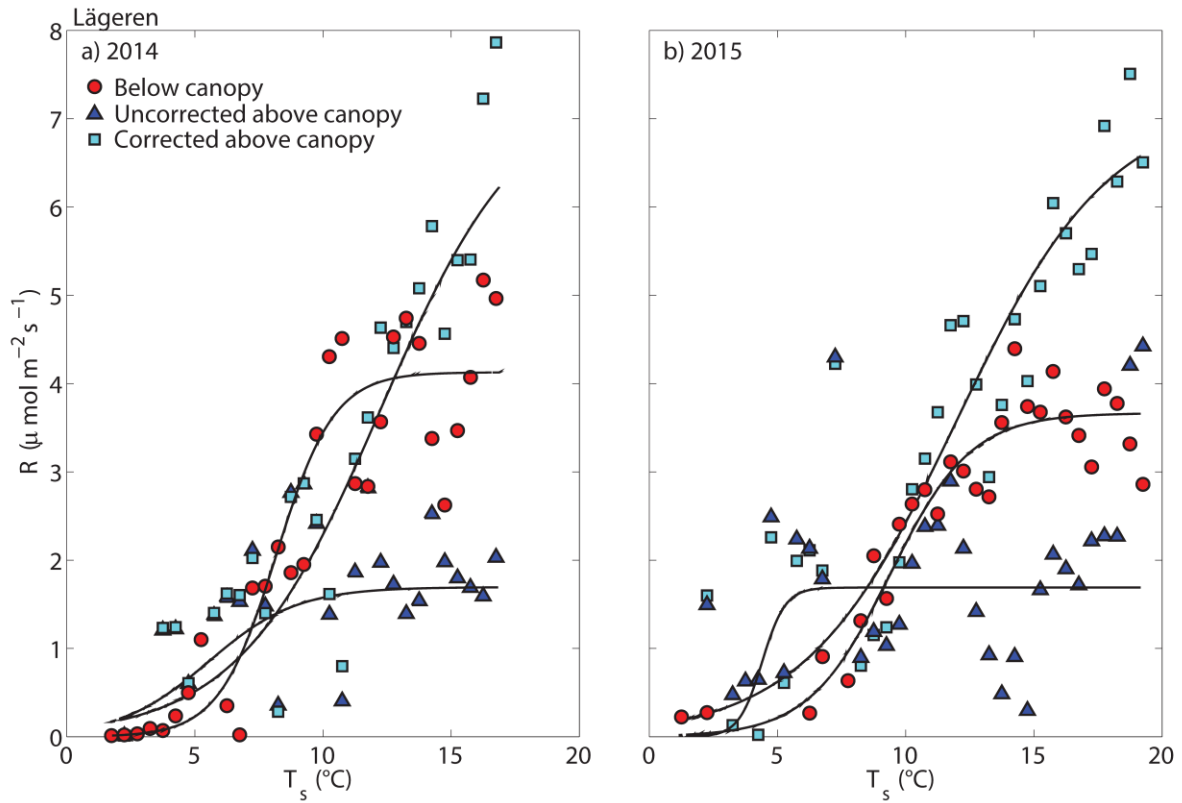


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937 **Figure 8:** Net ecosystem production (NEP, panel a), gross primary production (GPP, panel b)
 938 and respiration (*R*, panel c) above the canopy after the decoupling correction and below the canopy in 2014 and 2015. All lines are 5-
 939 day averages.

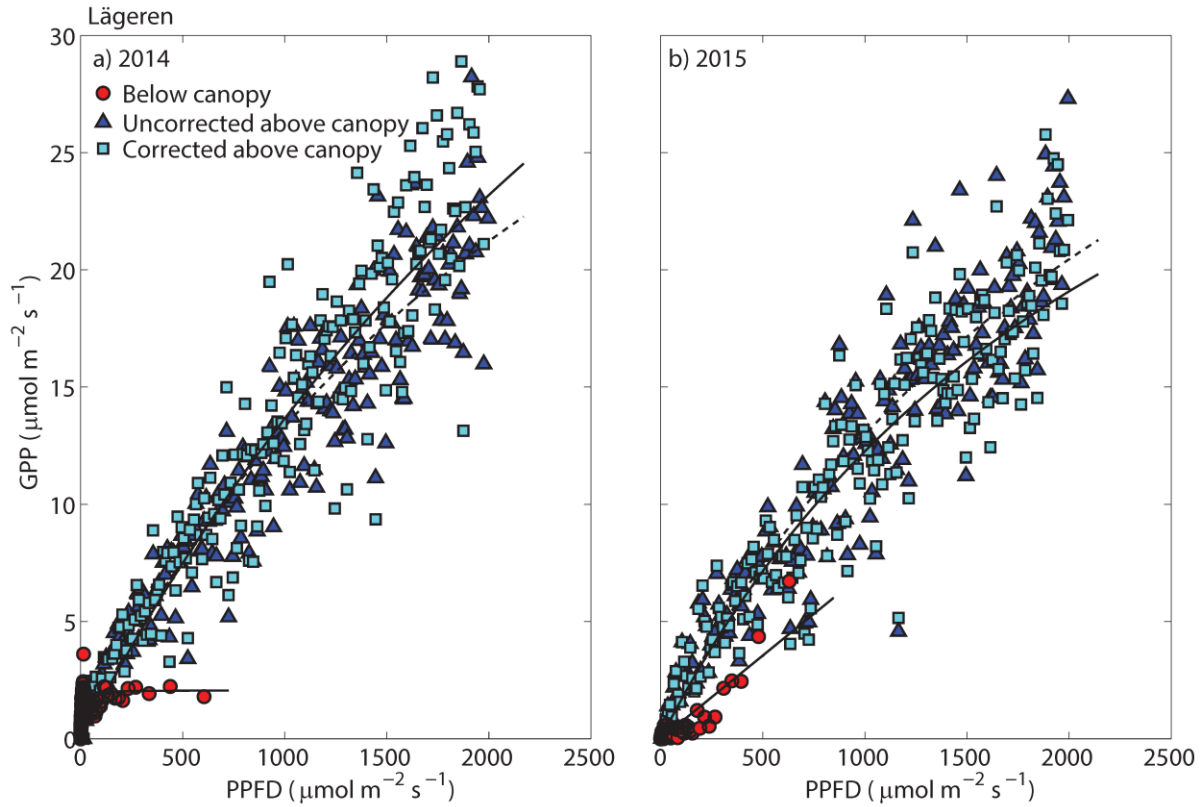
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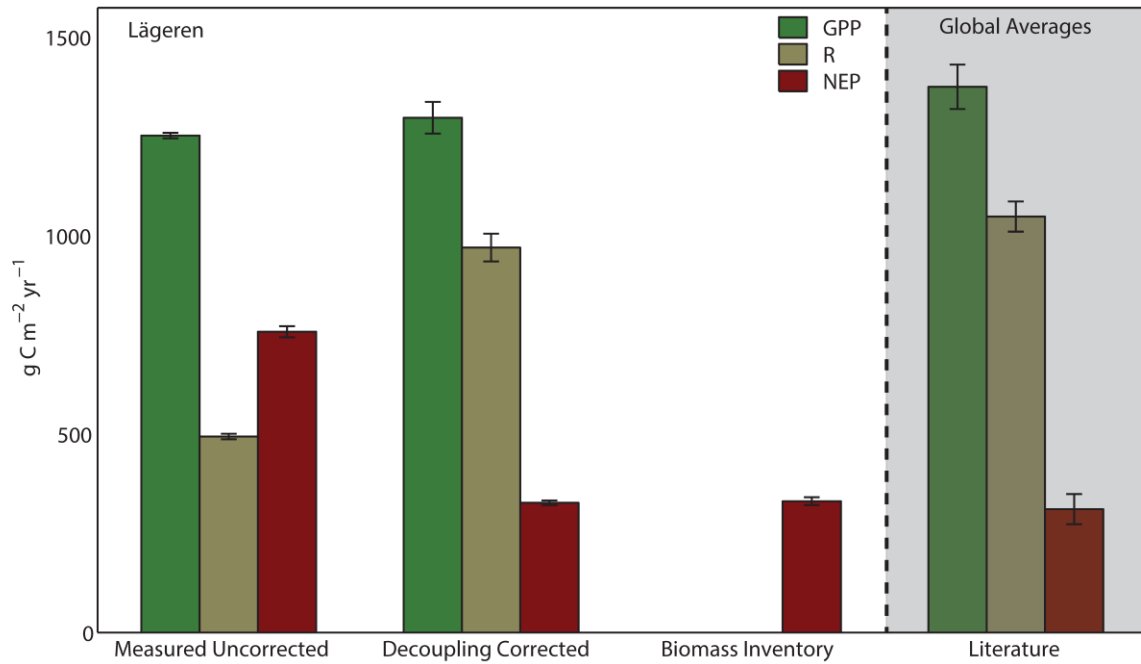
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 943 **Figure 9:** Respiration (R) versus soil temperature (T_s) at 5 cm depth at Lägeren in a) 2014 and b) 2015 for below
 944 canopy (red circles), uncorrected above canopy (blue triangles) and corrected above canopy (light blue squares). The
 945 lines are logistic equation (Eq. 1) fits to the measured half-hourly data (not binned) and the parameters are shown in
 946 Table 2. T_s values are binned in 0.5°C increments.

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 951 **Figure 10:** Gross primary production (GPP) as a function of downwelling photosynthetic photon flux density
 952 (PPFD) at Lägeren in a) 2014 and b) 2015 for below canopy (red circles), uncorrected above canopy (blue triangles)
 953 and corrected above canopy (light blue squares). The lines represent rectangular hyperbolic fits (Eq. 2) to the
 954 measured half-hourly data (not binned) and the values of the parameters are given in Table 3. PPFD values are
 955 binned in 50 μmol increments except for below-canopy values which are binned in increments of 50 values. The
 956 dashed line shows the uncorrected above canopy fit.

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Figure 11: Average annual ecosystem CO₂ fluxes at the Lägeren site as measured above canopy uncorrected, with decoupling correction, and from biomass inventories combined with models. The bars in the shaded area represent the global averages for temperate deciduous forest from the synthesis study from Luysaert et al. (2007). The bars represent the mean and error bars the standard deviation. Bars in green represent gross primary production (GPP), in brown represent respiration (R), and in red represent net ecosystem production (NEP).

997 **Tables**

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Table 1: Annual sums ($\text{g C m}^{-2} \text{ yr}^{-1}$) for below canopy, uncorrected above canopy, above canopy with decoupling correction, and below canopy percent contribution for net ecosystem production (NEP), gross primary production (GPP) and respiration (R) in 2014 and 2015.

Year	Flux ($\text{g C m}^{-2} \text{ yr}^{-1}$)	Below canopy uncorrected	Above canopy uncorrected	Above canopy corrected	Below canopy contribution with correction (%)
2014	NEP	-711	748	331	-
	GPP	187	1247	1325	14%
	R	898	499	995	90%
2015	NEP	-582	768	323	-
	GPP	57	1257	1269	4%
	R	639	489	945	68%
Mean \pm SE	NEP	-647 ± 65	758 ± 10	327 ± 4	-
	GPP	122 ± 65	1252 ± 5	1297 ± 28	9%
	R	769 ± 130	494 ± 5	970 ± 25	79%

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Table 2: Parameters for the logistic fits (Eq. 1) between respiration (R) and soil temperature (T_s) at Lägeren for below canopy, uncorrected above canopy and corrected above canopy fluxes. The logistic equation was fitted to the measured data in 2014 and in 2015.

		r_1 ($\mu\text{mol m}^{-2} \text{ s}^{-1}$)	r_2 ($^{\circ}\text{C}^{-1}$)	r_3 ($^{\circ}\text{C}$)	R^2
2014	Below canopy	4.13	0.89	8.18	0.64
	Uncorrected above canopy	1.70	0.58	5.52	0.46
	Corrected above canopy	7.40	0.36	12.24	0.81
2015	Below canopy	3.67	0.63	9.34	0.48
	Uncorrected above canopy	1.69	2.20	4.40	0.21
	Corrected above canopy	7.16	0.34	12.00	0.74

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Table 3: Parameters for the rectangular hyperbolic relationships between gross primary production (GPP) and photosynthetic photon flux density (PPFD) (Eq. 2) at Lägeren for below canopy, uncorrected above canopy and corrected above canopy fluxes. The equation was fitted to the measured data in 2014 and in 2015.

		α ($\text{mol C mol}^{-1} \text{ photons}$)	P_x ($\mu\text{mol m}^{-2} \text{ s}^{-1}$)	R^2
2014	Below canopy	0.45	2.07	0.46
	Uncorrected above canopy	0.02	52.40	0.82
	Corrected above canopy	0.02	76.82	0.78
2015	Below canopy	0.05	7.66	0.98
	Uncorrected above canopy	0.02	48.57	0.99
	Corrected above canopy	0.02	42.97	0.87

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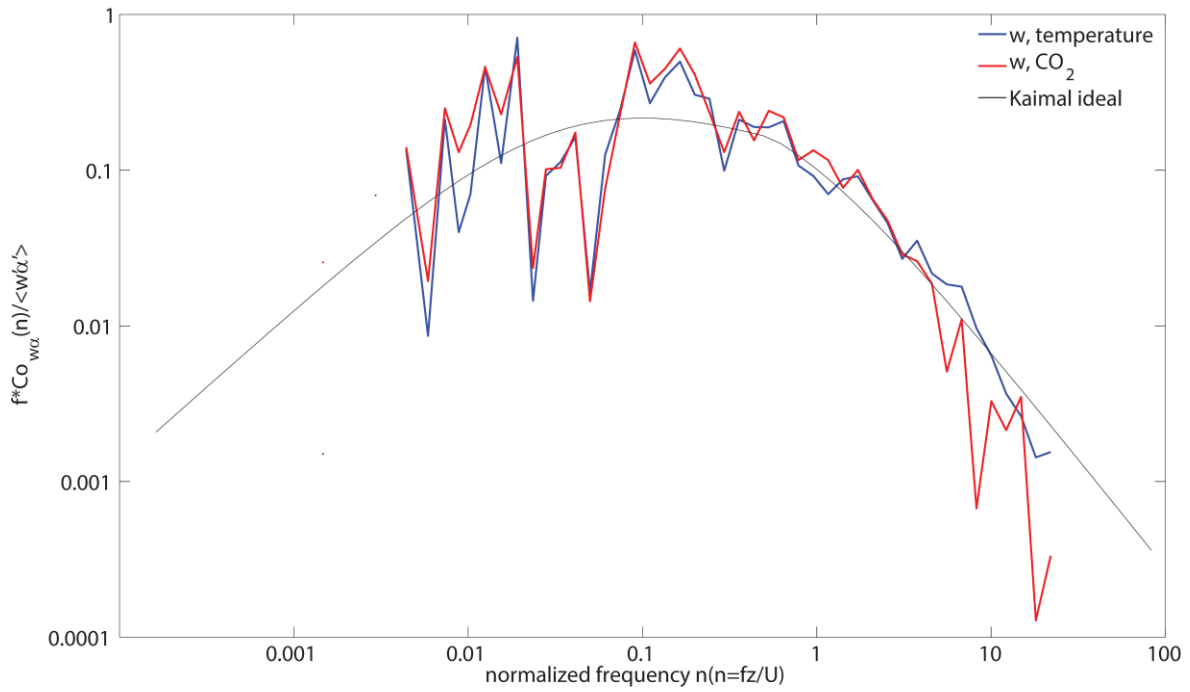
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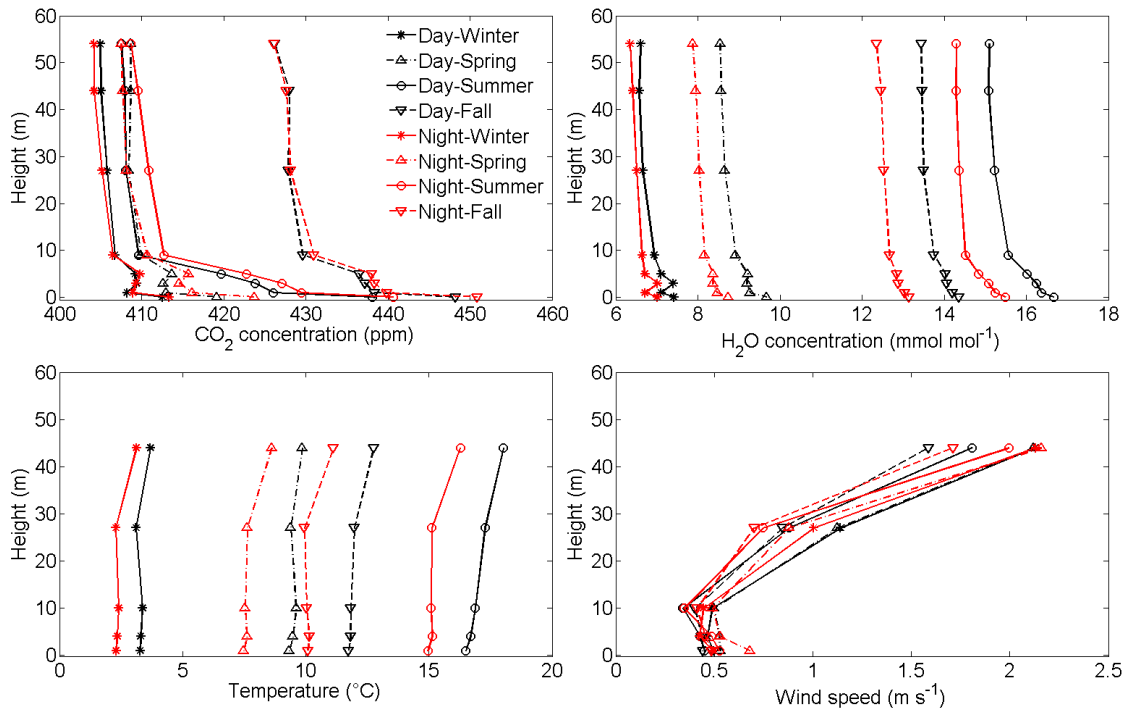
Table 4: Annual above-canopy net ecosystem production (NEP) at Lägeren in 2014 and 2015 without any correction, with a u_* threshold of 0.3 m s^{-1} , after accounting for 36% advection (according to Etzold et al. 2010), with the decoupling correction as well as NEP based on biomass inventories and modeled respiration.

NEP ($\text{g C m}^{-2} \text{ yr}^{-1}$)	No correction No u_*	No correction With u_*	No correction -36% advection	With correction No u_*	Biomass inventories and models
2014	748	501	477	331	321-341
2015	768	570	491	323	321-341
Mean \pm SE	758 ± 10	536 ± 35	484 ± 7	327 ± 4	331 ± 10

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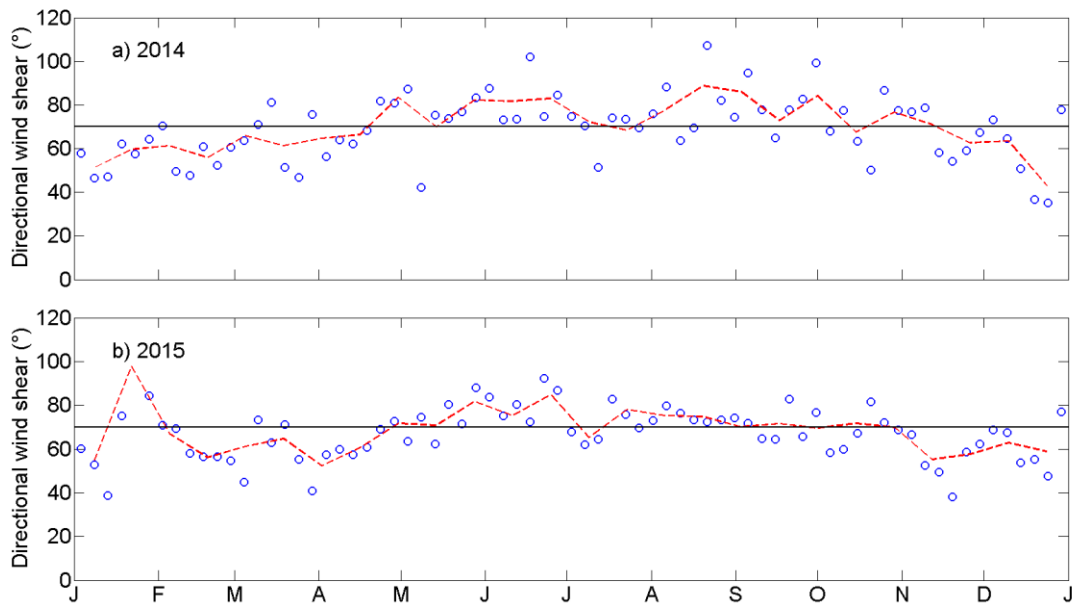


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 1018 **Figure S 1:** Typical below-canopy cospectra of vertical wind and temperature (blue line) and vertical wind and CO₂
 1019 (red line). The black line represents the ideal cospectra from Kaimal et al. (1972).
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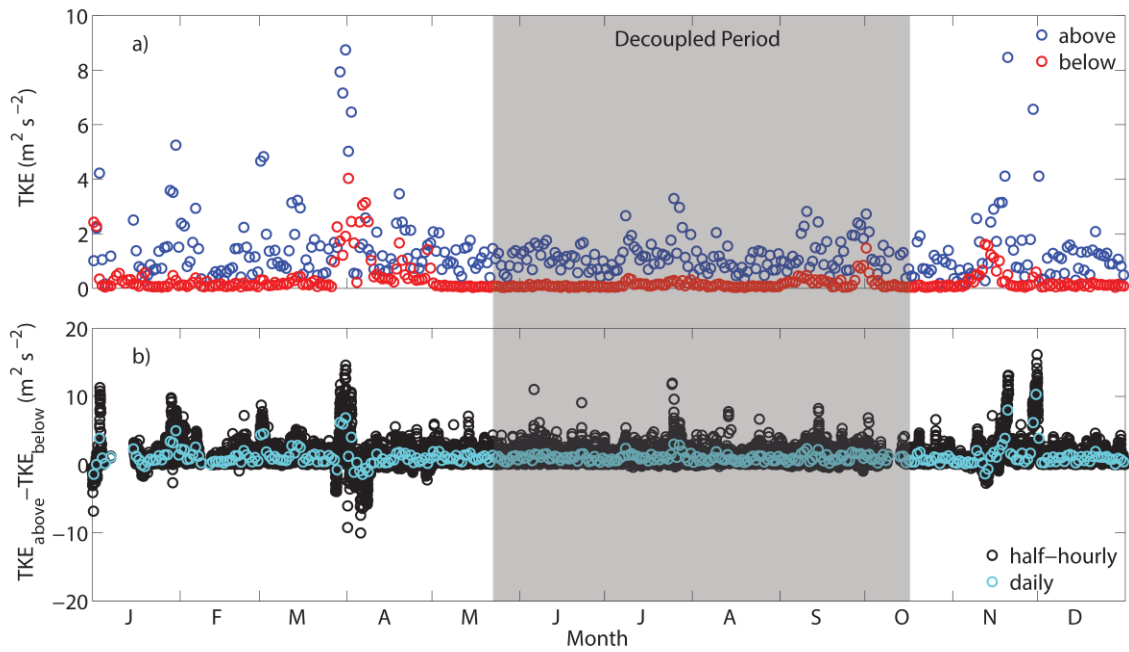


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1022 **Figure S 2:** Seasonal profiles of mean daytime (black) and nighttime (red) a) CO₂ concentration, b) H₂O vapor
 1023 concentration, c) temperature and d) wind speed within the canopy at Lägeren in 2014. Seasons are defined based on
 1024 the meteorological definition for winter (DJF), spring (MAM), summer (JJA) and fall (SON). The average tree
 1025 canopy height is 30 m, with the average tree canopy crown extending from 25 to 35 m.
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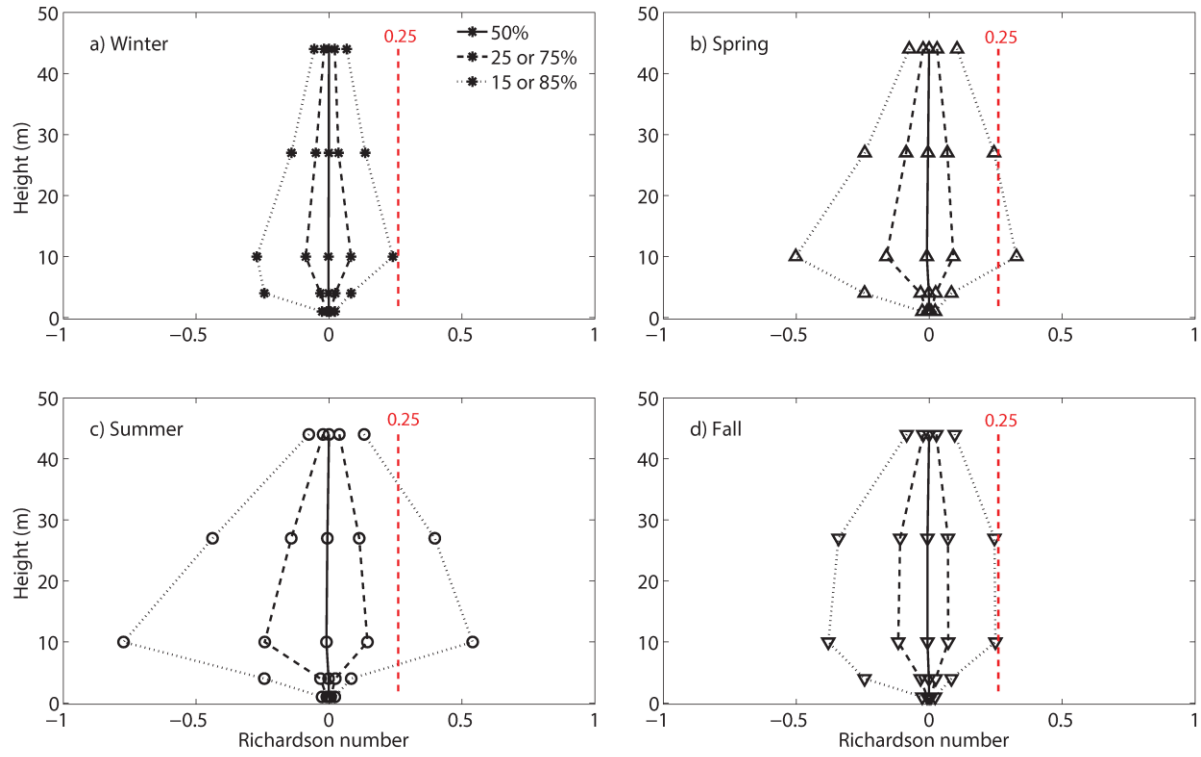


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 1028 **Figure S 3:** Directional wind shear at the Lägeren site in a) 2014 and b) 2015. The blue circles represent 5-day
 1029 averages and the red lines represent 14-day averages. The black line at 70° shows that wind shear during decoupled
 1030 periods tend to be greater than 70 degrees, although this is not consistent.
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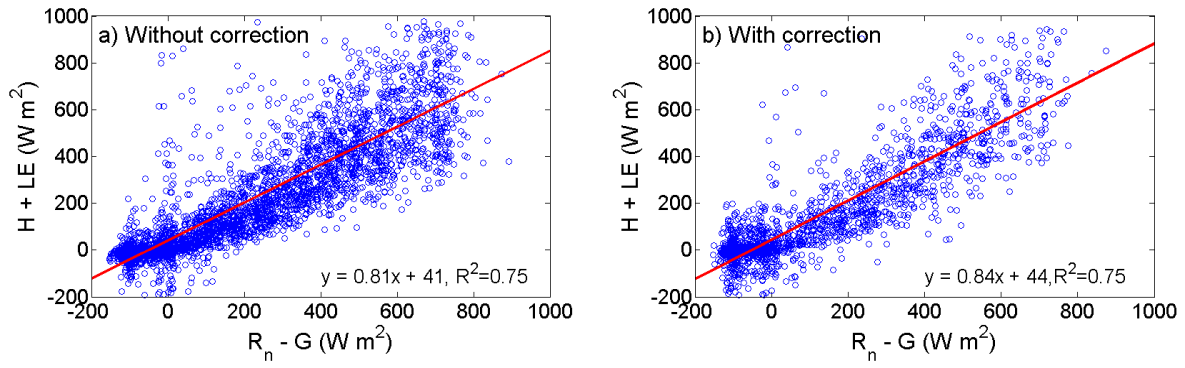
Figure S 4: Turbulent kinetic energy (TKE) a) above (blue) and below (red) the canopy, and b) difference in TKE above and below canopy in 2015. The circles in panel a) represent daily averages. The black circles in panel b) represent the half-hourly data while the cyan circles represent daily averages. The shaded area represents the decoupled period.



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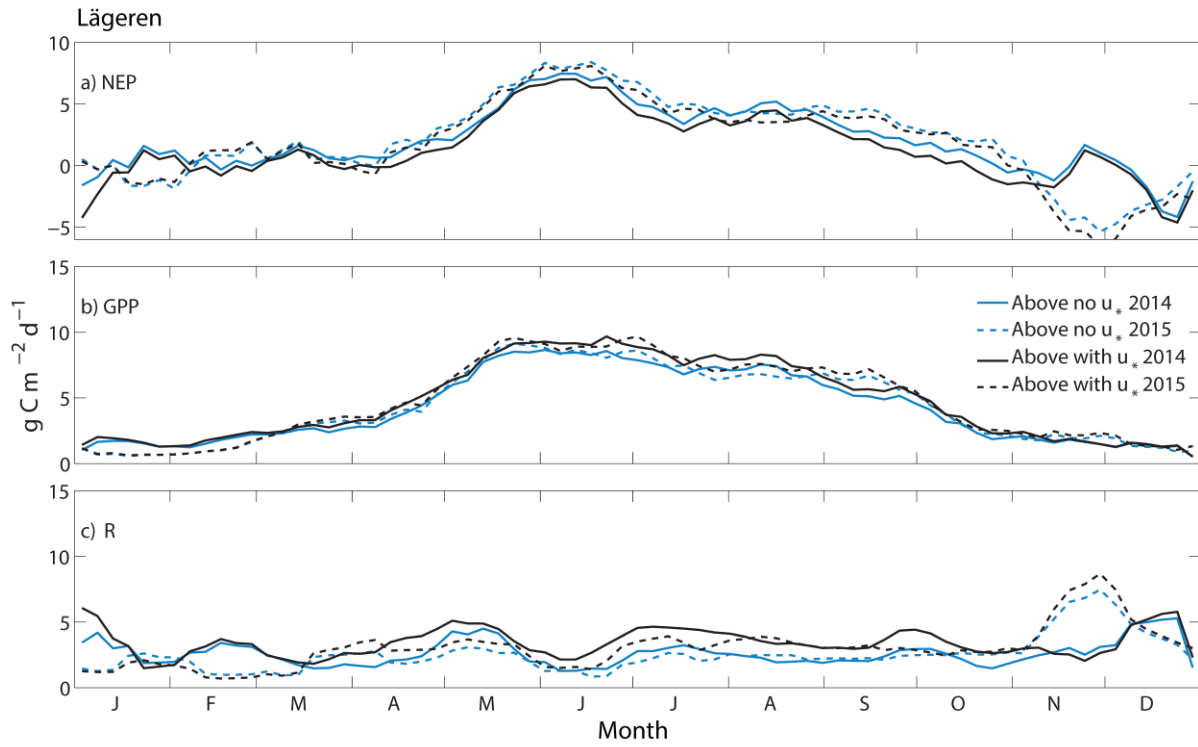
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Figure S 5: Richardson numbers in a) winter, b) spring, c) summer, and d) fall. The red line at 0.25 shows the critical Richardson number. The filled line shows the mark for 50% of the data, the dashed line for 25% and 75% of the data, and the dotted line for 15 and 85% of the data.



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Figure S 6: Energy balance closure a) without the decoupling correction and b) with the decoupling correction during the decoupled period in 2014.



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 1048 **Figure S 7:** Net ecosystem production (NEP), gross primary production (GPP) and respiration (R) above the canopy
 1049 without (blue lines) and with (black lines) the u_* filtering in 2014 and 2015. All lines are 5-day averages.
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