CO₂ exchange and component CO₂ fluxes of a boreal Scots pine forest

Pasi Kolari¹, Liisa Kulmala¹, Jukka Pumpanen¹, Samuli Launiainen², Hannu Ilvesniemi³, Pertti Hari¹ and Eero Nikinmaa¹

¹) Department of Forest Ecology, P.O. Box 27, FI-00014 University of Helsinki, Finland
²) Department of Physics, P.O. Box 64, FI-00014 University of Helsinki, Finland
³) Finnish Forest Research Institute, Vantaa Research Unit, P.O. Box 18, FI-01370 Vantaa, Finland

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We studied CO₂ fluxes derived from eddy covariance (EC), modelled with a stand photosynthesis model, and upscaled from continuous measurements with chambers in a Scots pine stand. The annual photosynthesis (GPP_EC), ecosystem respiration (R_e_EC) and net CO₂ exchange (NEE_EC) derived from EC were correlated with each other. Soil CO₂ efflux dominated R_e for the whole year, most clearly in winter. The relative contributions of the above-ground respiration components were largest in spring and early summer. The respiration components generally followed the seasonal patterns of temperature although temperature-normalised respiration was higher in the growing season than in winter. The respiration components showed parallel decline during drought. Interannual variability in the annual chamber-based CO₂ budgets was twice as large as in the EC-based fluxes, the uncertainty in the chamber fluxes was also larger. Using different environmental drivers for estimating R_e from NEE_EC affected the annual R_e_EC and GPP_EC ±4%.

Introduction

Carbon balance of a forest results from photosynthetic production or Gross Primary Production (GPP), respiratory losses from plant metabolism (autotrophic respiration) and from the microbial decomposition of dead plant biomass (heterotrophic respiration). The responses of these processes to environmental drivers are different in short term and over the seasons and reflect also the long-term development of the forest structure.

The responses of photosynthesis to light and temperature in short term are relatively well understood (Farquhar and von Caemmerer 1982). The function of stomata has been described as a response to evaporative demand and radiation and as a feedback from photosynthesis to maintain leaf internal CO₂ (e.g. Ball et al. 1987) or by applying the principle of plants maximising CO₂ uptake minus transpiration cost (Hari et al. 1986, Berninger et al. 1996). The availability of plant extractable water in soil explains well the relative transpiration rate under drought (Duursma et al. 2007). In boreal evergreen conifers the seasonal cycle of photosynthetic capacity (maximum light-saturated photosynthesis) can be described accurately as a

The respiratory CO₂ effluxes of a forest ecosystem are driven by several factors like air and soil temperature, soil water content and the availability and the quality of substrate for respiration (review in Ryan and Law 2005). Despite that, respiration is frequently analysed as a process solely driven by temperature and, in case of below-ground respiration, also by soil moisture (e.g. Davidson et al. 1998, Skopp et al. 1990). Zha et al. (2007) observed that CO₂ efflux from the soil is the dominant component of ecosystem respiration (Rₑ) in a boreal Scots pine forest, and differences between years in soil CO₂ efflux could be explained by differences in temperature during the growing season.

Through an analysis of European eddy-covariance fluxes, Reichstein et al. (2007) found that the variation in annual GPP was largely compensated by parallel changes in Rₑ. Autotrophic respiration increases with GPP as there is more substrate available for respiration (Janssens et al. 2001, Ryan and Law 2005). Dewar et al. (1998) suggested that because respiration ultimately depends on supply of substrate from photosynthesis, they should remain proportional when integrated over long periods of time. Plant respiration has been shown to acclimate to changing temperature regimes (Atkin and Tjoelker 2003) and it is possible that the ratio between plant respiration and photosynthesis is maintained in long term (e.g. Gifford 2003). Thus, respiration dynamics should be analysed starting from the functional connection between the source of substrate for respiration, i.e. production of sugars in photosynthesis, and the need of energy for construction and maintenance of plant tissues. This is not trivial, however, because the mechanisms behind within-tree carbon allocation are still poorly known (Sievänen et al. 2001) and the relationships between GPP and respiration often do not match in short term (e.g. Tang et al. 2005). The interpretation of observed CO₂ effluxes at any given moment is also difficult since the contributions of different respiration processes can vary diurnally and seasonally.

Recent research on forest ecosystem carbon balances has often been based on measurements of net CO₂ exchange of the ecosystem by eddy covariance. Eddy-covariance-based component fluxes, however, give little information on the partitioning of CO₂ uptake between the trees and the understory vegetation, or on the relative magnitudes of above- and below-ground respiration components or root and microbial respiration. Continuous small-scale flux measurements, as monitoring of leaf CO₂ exchange by chambers, may prove invaluable in analysing the contributions of different functional compartments to the forest ecosystem CO₂ exchange. Parallel use of ecosystem level and small-scale fluxes opens new possibilities in distinguishing the origins of short- and long-term variations in NEE.

Fluxes measured at a small spatial scale must be upscaled to the stand level using the available information on the spatial variation of environmental driving factors and the distribution of different CO₂ sinks and sources within the ecosystem. Exact correspondence between the eddy covariance and the upscaled fluxes is very difficult to achieve due to the heterogeneity of a forest mosaic and the temporally varying source area (footprint) of eddy covariance. Comparison of EC-based fluxes with upscaled or modelled fluxes is also hampered by the uncertainties in the measured NEE itself (e.g. Aubinet et al. 2000), by the methods used in replacing the missing or rejected measurements (Falge et al. 2001, Moffat et al. 2007), and in deriving the component fluxes, GPP and Rₑ, from the measured NEE (Stoy et al. 2006). There is no standard way to estimate GPP and Rₑ and they are also dependent on each other; a method that yields biased Rₑ unavoidably results in biased GPP. The systematic errors in determining GPP and Rₑ from eddy covariance have received fairly little attention, partly due to the difficulty in evaluating the accuracy of the component fluxes using the measured NEE itself. Independent chamber-based observations on the component CO₂ fluxes will help in estimating the accuracy of different EC-based Rₑ and GPP estimates.

In this paper we quantify the annual net CO₂ exchange and the component CO₂ fluxes (photosynthesis of trees and ground vegetation, respiration of foliage and wood, soil CO₂ efflux) of a coniferous forest stand in southern Finland. We also determine the seasonal and interannual variability in the partitioning of the net ecosys-
tem CO₂ exchange and analyse the within-year and year-to-year variability in the responses of the component fluxes to the environmental driving factors. Finally we evaluate the random and systematic errors involved in the integration of the chamber-based fluxes and in deriving the component fluxes from the measured net ecosystem exchange.

Material and methods

Site characteristics

The measurement site is located in southern Finland (61°51´N, 24°17´E, 180 m a.s.l.) at the SMEAR II field station (Hari and Kulmala 2005). The site was established in 1962 by sowing after prescribed burning and mechanical soil preparation. The soil is a Haplic podzol on glacial till (FAO-Unesco 1990). The site is of medium fertility and dominated by Scots pine (Pinus sylvestris) with sparse understory of Norway spruce (Picea abies) and scattered deciduous trees. This study concentrates on the carbon balance of the SMEAR II stand in years 2002–2007. In 2006 the mean height of the stand within 150-m radius from the eddy-covariance mast was 16.3 m and tree (diameter at 1.3 m height > 5 cm) density 1400 ha⁻¹. The seasonal maximum of the foliage mass in pine and spruce was 4500 kg ha⁻¹ in 2002 and it increased to 4800 kg ha⁻¹ by 2006 (Ilvesniemi et al. 2009). These biomasses correspond to all-sided leaf area index (LAI) of 6 and 6.5, respectively (Palmroth and Hari 2001). Outside the 150-m radius the stand was slightly denser with a larger proportion of spruce and deciduous trees. The ground vegetation consisted mostly of dwarf shrubs blueberry (Vaccinium myrtillus) and lingonberry (Vaccinium vitis-idaea), feather moss (Pleurozium schreberi) and other bryophytes. The foliage biomass of the ground vegetation varied between 680 and 990 kg ha⁻¹ from year to year (Ilvesniemi et al. 2009).

Measurements of CO₂ fluxes

Fluxes from an automated chamber system were available for the years 2002–2006. The shoot chambers were acrylic plastic boxes with volume of 1 dm³. The chambers were open most of the time exposing the chamber’s interior to the ambient conditions. For measuring fluxes, the chambers were closed intermittently for one minute, 70–100 times a day. More detailed descriptions of the instrumentation and the flux calculation are provided by Altimir et al. (2002) and Hari et al. (1999). The shoots were always debudded before the chamber installation, i.e. further elongation of the shoots was prevented. The number of shoots being monitored simultaneously was 3–4, each shoot was kept under monitoring for about two years.

Respiration of tree stems was studied using two acrylic plastic chambers (height 20 cm, width 3.5 cm) attached to the bark of one tree. The efflux of CO₂ from the stem was monitored hourly. The measurements were started in June 2002. The spatial variability of CO₂ efflux per unit stem surface area was determined by circulating the chambers between different heights and different trees for several weeks in the summer of 2003. The chambers were then positioned in a way that represented the whole stem as well as possible: one chamber in the lower part of the living crown and the other 2–3 m lower, just below the crown. The chambers were moved upwards every second year to maintain their positions relative to the crown base.

Continuous monitoring of CO₂ efflux from the forest floor was carried out hourly with three transparent soil chambers (diameter and height 20 cm). The measuring system was described in detail by Pumpanen et al. (2001), and its accuracy was evaluated by Pumpanen et al. (2004). One of the chambers was permanently in the same location in 2002–2006; the others were moved to new locations twice during the year 2006. As the spatial variation in soil CO₂ effluxes is large, measurements at more than three locations are needed to improve the accuracy of the CO₂ efflux per unit ground area in the whole stand. Therefore, we made additional flux measurements with a manually operated chamber (Kolari et al. 2004) at 14–20 locations within the stand and in 5–8 campaigns during each summer.

The ecosystem CO₂ exchange was measured with a closed-path eddy-covariance measuring system. The anemometer and the sample air
intake were installed above the stand at a height of 23 m. The instrumentation was documented in more detail in Vesala et al. (2005). The topography and micrometeorological conditions of the site as well as the processing of the raw data to half-hourly averaged fluxes were described by Rannik (1998).

Estimation of photosynthesis in trees and ground vegetation

Photosynthetic production of the coniferous trees was determined by integrating the instantaneous photosynthetic rate at shoot level over the whole stand. The integration was done with SPP (Stand Photosynthesis Program, Mäkelä et al. 2006) that combines a model of shoot photosynthetic production with the model of light interception in the canopy (Stenberg 1996) and soil water limitation to gas exchange (Duursma et al. 2007). In SPP, photosynthetic production is modelled at tree level. Trees of different species, size, leaf area density or physiology are represented as size classes. Each size class may have its own photosynthetic parameters, canopy shape and dimensions. The individual crowns consist of a homogeneous medium. The trees are assumed to be randomly distributed in the stand. When calculating the light environment inside the crowns, shading by the neighbouring trees is taken into account in addition to within-crown shading.

The photosynthesis component of SPP consists of the optimal stomatal control model (Hari et al. 1986) and the annual cycle model (Mäkelä et al. 2004). The key parameter in the optimal stomatal control model is photosynthetic efficiency \( \beta \) (light-saturated photosynthesis per unit leaf internal CO₂) that varies seasonally. The daily values of \( \beta \) were obtained with two different methods.

In the first method, the daily values of \( \beta \) were predicted from the temperature history \( S \) that follows temperature \( T \) in a delayed manner: if \( T \) is held constant, \( S \) approaches \( T \), and if \( T \) is changed, \( S \) will move toward the new temperature with a time constant \( \tau \)

\[
\frac{dS}{dt} = \frac{T - S}{\tau} \tag{1}
\]

The values of \( \beta \) were calculated as a sigmoid function of \( S \) using parameter values taken from Kolari et al. (2007). The values of \( \beta \) obtained from \( S \) were further multiplied by a daily factor ranging between 0 and 1 to take into account the carry-over effect of nighttime frost (Mäkelä et al. 2004, Kolari et al. 2007). The value of the frost modifier was 1 if the minimum air temperature during the previous night was above zero. Below 0 °C the modifier decreased linearly with temperature, reaching zero at –10 °C.

The second method involved estimation of daily \( \beta \) directly from the measured shoot CO₂ exchange. The values of \( \beta \) were estimated from the net CO₂ exchange of the experimental shoots, i.e. gross photosynthesis depends on how daytime respiration is calculated. Seasonal variation in the temperature response of respiration was taken into account by estimating the temperature response function from nighttime shoot chamber measurements in a moving time window (see documentation of respiration further below). \( \beta \) was then estimated from daytime data using the obtained respiration parameters. The absolute level of summertime light-saturated photosynthesis varied considerably among the experimental shoots due to shoot-to-shoot variation in physiology and needle architecture (e.g. needle angles, dimensions and density, overlapping of needles in the chamber) as well as due to inaccuracy in determining the needle surface area inside the chambers (Kolari et al. 2007). Therefore, the shoot-specific annual courses of \( \beta \) were scaled so as to match the average value of \( \beta \) from 15 June to 15 July for all shoots and years used in this study.

Canopy GPP estimated with the parameter \( \beta \) calculated from temperature history will be hereafter called “predicted GPP” whereas GPP upscaled directly from the chambers will be referred as “chamber-based GPP”. In both approaches the values of the other photosynthetic parameters were based on the mean values of several shoots and years (Kolari et al. 2007).

Seasonal variation in the stand foliage area (LAI) was approximated from shoot growth observations: Foliage area is at its minimum in winter and spring, starts growing linearly in the beginning of June, stabilises to its maximum value for July and August and declines to its
minimum during September when the oldest age class of needles is shed. The annual turnover of foliage was 25% of the maximum of foliage mass each year. Due to the stand growth (Ilvesniemi et al. 2009) the seasonal minimum of LAI thus increased linearly from 4.5 in 2002 to 4.9 in 2006.

Photosynthetic production was integrated over the years 2002–2006 in half-hour time steps, using half-hourly averaged incident PAR measured above the canopy and temperature and gas concentrations measured inside the canopy at 8 m height as the driving factors. Volumetric soil water content in the uppermost 10 cm of the mineral soil was converted to water tension from pF curves measured at the site (Mecke et al. 2002). The soil water tension was used to calculate the maximum rate of transpiration (degree of stomatal opening) that can be sustained without leaf water potential decreasing below a threshold value of –2 MPa (Duursma et al. 2007). In the chamber-based GPP, the effect of soil water on gas exchange was omitted because it was embedded in the photosynthetic parameters. There were short gaps in the chamber data caused by maintenance, power supply breaks, or instrument malfunction. When calculating the annual C budgets, the missing daily chamber-based GPPs were replaced with the annual regression of chamber-based GPP on predicted GPP.

Photosynthetic production of the ground vegetation was determined with an empirical model (Kolari et al. 2006) that integrates momentary photosynthetic rate over space and time to the stand level. In the integration procedure, we used the species-specific photosynthetic light response functions, the yearly measured biomass distributions of the ground vegetation species, and the modelled spatial distributions of irradiance at the forest floor. Photosynthetic light responses were determined using manually operated opaque and transparent closed dynamic chambers (more details in Kulmala et al. 2008). The measurements were taken at about two-week intervals during the growing season of 2003. The difference between the dark and the transparent chamber fluxes directly gives photosynthetic rate of the plot being measured. Four to five intermediate light intensities were generated by shading the transparent chamber with layers of netted fabric. Photosynthesis $P$ was modelled as a saturating function of photosynthetically active radiation $I$ measured inside the chamber

$$P = \frac{P_{\text{max}} I}{I + b}$$

(2)

The photosynthetic parameters, light-saturated rate of photosynthesis ($P_{\text{max}}$) and curvature $b$, were determined separately for blueberry, lingonberry, heather (Calluna vulgaris), grasses and moss. The seasonal patterns of $P_{\text{max}}$ were previously found to be similar to the photosynthetic efficiency of Scots pine (Kolari et al. 2006). Daily values of $P_{\text{max}}$ were thus calculated using the same annual cycle model as was used for the Scots pine canopy, the values measured in July representing the annual maxima of $P_{\text{max}}$. Photosynthesis under snow was assumed to be zero.

**Respiration of foliage and wood and CO₂ efflux from the soil**

The measured component CO₂ fluxes were used to determine the respiration of tree foliage including twigs ($R_{\text{shoot}}$), CO₂ efflux from the stems and branches ($R_{\text{stem}}$), and CO₂ efflux from the soil ($R_{\text{soil}}$). Measuring intervals with the chambers were varying; therefore, we calculated half-hourly respiration components and filled the gaps in the measurements using empirical exponential temperature regression:

$$R = R_{10} Q_{10}^{(T-10)/10}$$

(3)

where $R_{10}$ is the base level of respiration, i.e. respiration at 10 °C, and $Q_{10}$ the temperature sensitivity, i.e. the slope of the apparent temperature response of respiration. The base level of respiration varies during the year due to, for instance, varying proportions of maintenance and growth respiration. We took into account this variation, not directly related to temperature, by applying similar procedures in compiling half-hourly data sets of the component fluxes: short-term temperature sensitivity of respiration was fixed and the base level estimated daily in a time window of 3–7 days.
Respiration of Scots pine foliage was calculated using a modified version of Eq. 3 (Mäkelä et al. 2006):

\[
R_{\text{stem}} = \max \left[ 0, r_{\text{r}} Q_{10}^{(T-10)/10} + c_r \right] \quad (4)
\]

where \( c_r \) is a parameter that forces respiration to zero at \(-5 \, ^\circ\text{C}\). \( Q_{10} \) was assumed to be constant over the year and determined from measurements in June 2004.

Respiration of the ground vegetation at SMEAR II was embedded in the CO₂ efflux from the soil and not estimated separately. Short-term temperature sensitivity \( Q_{10} \) of \( R_{\text{soil}} \) was determined by selecting rainless 10-day periods from spring, summer and autumn of 2004 and calculating regressions of nighttime soil CO₂ efflux on temperature measured at different depths (Eq. 3). We used the mean of temperatures measured in the 5-cm thick organic layer and in the uppermost 5 cm of the mineral soil as the explanatory factor (Pumpanen et al. 2003a).

The measured stem CO₂ effluxes were used for deriving an exponential relationship (of the same form as Eq. 3) between temperature and the CO₂ efflux in order to construct a continuous time series of fluxes. Local CO₂ production by respiration inside the stem follows in short term temperature that lags slightly behind air temperature. CO₂ efflux from the stems in turn lags behind the actual CO₂ production because diffusion out of the stem is slow. The stem CO₂ efflux was modelled as a response to temperature \( T_{\text{stem}} \) that follows air temperature \( T_{\text{air}} \) with a time constant \( \tau \) of 4 hours:

\[
\frac{dT_{\text{stem}}}{dt} = \frac{T_{\text{air}} - T_{\text{stem}}}{\tau} \quad (5)
\]

Note that \( T_{\text{stem}} \) is not the actual bole temperature. In addition to describing the slowness of heat transfer into the respiring tissues in the stem, the time lag in the diffusion of CO₂ out of the stem is embedded in the time constant. \( Q_{10} \) was first determined by fitting the respiration model to chamber measurements pooled over June 2004. The seasonal course in the base level of respiration was then estimated daily in a seven-day moving time window of stem CO₂ efflux data. The fluxes before the deployment of the stem chambers in June 2002 were estimated using the mean seasonal course in the base level of stem CO₂ efflux in 2004–2005.

The obtained rates of CO₂ release per unit needle surface area were multiplied by the total needle area per m² ground in the stand. Stem CO₂ effluxes in the stand were calculated by multiplying the efflux per stem surface area by the total stem and branch surface area (0.5 m² m⁻² ground) in the stand. Soil chambers give directly flux per ground surface area but the fluxes were corrected for spatial variation using the manual chamber data.

### Net ecosystem exchange, photosynthesis and respiration from eddy covariance

The half-hourly averaged NEE EC were accepted or rejected using the turbulence criteria described in Markkanen et al. (2001). The accepted fluxes were further corrected for half-hourly changes in storage of CO₂ below the measuring height. The NEE EC was partitioned into \( R_{\text{e,EC}} \) and GPPEC. \( R_{\text{e,EC}} \) was modelled using an exponential equation (equivalent to Eq. 3) with temperature at a depth of 2 cm in the soil organic layer as the explanatory factor. The accepted half-hourly fluxes were used for deriving GPPEC directly from the measured NEE EC as

\[
\text{GPP EC} = -\text{NEE EC}_c + R_{\text{e,EC}} \quad (6)
\]

When NEE EC was missing or rejected, GPPEC was replaced by empirically modelled ecosystem photosynthesis \( P_e \):

\[
P_e = \frac{1}{2\theta} \left[ \frac{\alpha I + P_{e,\text{max}}}{\sqrt{(\alpha I + P_{e,\text{max}})^2 - 4\theta \alpha I P_{e,\text{max}}}} \right] \quad (7)
\]

where \( I \) is incident photosynthetically active radiation (PAR), \( P_{e,\text{max}} \) the rate of saturated photosynthesis, \( \theta \) a parameter defining the convexity of the light response curve, and \( \alpha \) the initial slope of the curve. The model was parameterised using GPPEC obtained directly from accepted fluxes.

The temperature sensitivity of \( R_{\text{e,EC}} \) was derived from the regression of accepted nighttime NEE EC on temperature in the soil organic layer over the summer of 2004. To take into account the
interannual and seasonal variations in the photosynthetic light response and \( R_{e,EC} \), the base level of ecosystem respiration (\( R_{10} \) in Eq. 3) and the parameters \( \alpha \) and \( P_{e,max} \) in the GPP model were estimated daily using a 9-day moving window of accepted flux data (5-day window during the drought in July and August 2006). The parameters values were calculated iteratively: \( R_{10} \) was first estimated from flux measurements at low light (PAR < 300 \( \mu \)mol m\(^{-2}\) s\(^{-1}\)) within the time window using photosynthetic parameters from the previous time window. The obtained value of \( R_{10} \) was then used in estimating new values for \( \alpha \) and \( P_{e,max} \) from daytime (solar elevation angle > 0\(^{\circ}\)) data. This iteration was continued until the parameter values converged to pre-defined accuracy. In low light the simultaneous estimation of \( P_{e,max} \) and \( \alpha \) tends to lead to spurious values. Therefore, the \( P_{e,max}/\alpha \) ratio, i.e. the curvature of the photosynthetic light response was smoothed over the year as running average over 60 days, and daily values of \( R_{10}, \alpha \) and \( P_{e,max} \) were re-estimated using the fixed seasonal course of \( P_{e,max}/\alpha \). The same values of \( \theta \) and the temperature sensitivity of \( R_e \) were used for all years.

The systematic uncertainties in the flux estimates were analysed by using different types of temperature as the explanatory factors in the \( R_e \) model. Besides the organic layer temperature, we used air temperature measured at 8 m height and temperature at the depth of 5 cm in the mineral soil (about 10 cm from the ground surface).

### Ancillary data

PAR was measured above the canopy at 23 m height and recorded every minute. Vertical profiles of air temperature and gas concentrations (\( \text{CO}_2 \) and \( \text{H}_2\text{O} \)) were measured at several heights at intervals of 1–6 minutes, records taken at 8 m height were used in this study. Soil moisture was measured with TDR method and temperature with silicon sensors. Measurements at five plots in the stand, each accommodating several sensors at different depths, were averaged for the organic layer and for each mineral soil layer (A, B, C). Vesala et al. (2005) and Pumpanen et al. (2003b) describe the meteorological and the soil measurements in more detail.

The meteorological and the soil data were averaged half-hourly. The gaps in the data were normally no longer than few hours and could be filled by linear interpolation. In case of soil moisture and temperature, this was the standard for gaps up to 24 hours. In radiation, air temperature, and gas concentrations, gaps longer than four hours were filled with the mean diurnal course of the missing variable in a time window that included one full day of data before and after the gap. Sometimes it was possible to recover the missing data from the other measuring systems such as the chambers.

We used air temperature to determine the beginning of the growing season for each year. The beginning of the growing season was defined as the date when the daily mean temperature reached 5 °C and stayed above zero thereafter.

### Results

#### General weather patterns

The environmental factors at SMEAR II showed systematic seasonal variation typical of the boreal zone (Fig. 1). The year 2002 had a warm and sunny summer but the winter started early and the dry soil froze deeper than normally during the winter. The soil moisture was shortly low again in September 2003. The beginning of May in 2004 was very warm but the weather rapidly cooled down, the rest of the summer was rainy and slightly cooler than average. In late summer of 2006 there was prolonged drought. The late autumn and early winter (November–December) of 2006 were exceptionally warm, the warm winter continued until March 2007. The summer of 2007 was rainy. The annual climatic factors and \( \text{CO}_2 \) fluxes from eddy covariance are summarised in Table 1.

### Magnitude and partitioning of ecosystem \( \text{CO}_2 \) exchange

Correspondingly to the seasonal variation in the environmental factors, the absolute levels and the partitioning of the component \( \text{CO}_2 \) fluxes
varied considerably (Figs. 2 and 3). All CO₂ fluxes were very small in winter, increased in spring, peaked in the midsummer and diminished again in autumn.

The maximum upscaled canopy GPP on summer days was roughly 20 μmol m⁻²(ground) s⁻¹, the chamber-based and predicted GPP estimates were very close to each other. The midday ground vegetation GPP in the summer was an order of magnitude smaller, about 2 μmol m⁻² s⁻¹. The respiration of tree foliage and twigs in the summer nights was typically 1.5–2

Table 1. Climatic factors at SMEAR II and annual CO₂ fluxes with their approximated uncertainties (g C m⁻² a⁻¹) from eddy covariance. The uncertainties of the CO₂ fluxes are separated into a random component that originates from the noise in the half-hourly fluxes, and a systematic component caused by bias in the flux measurements.

<table>
<thead>
<tr>
<th>Year</th>
<th>Mean T (°C)</th>
<th>Precipitation¹⁾ (mm)</th>
<th>Growing season start date</th>
<th>GPP_EC</th>
<th>R_EC</th>
<th>NEE_EC</th>
</tr>
</thead>
<tbody>
<tr>
<td>2002</td>
<td>4.2</td>
<td>535</td>
<td>20 Apr.</td>
<td>1084</td>
<td>850</td>
<td>−232</td>
</tr>
<tr>
<td>2003</td>
<td>4.1</td>
<td>645</td>
<td>4 May</td>
<td>974</td>
<td>833</td>
<td>−136</td>
</tr>
<tr>
<td>2004</td>
<td>4.1</td>
<td>718</td>
<td>16 Apr.</td>
<td>1068</td>
<td>836</td>
<td>−225</td>
</tr>
<tr>
<td>2005</td>
<td>4.4</td>
<td>698</td>
<td>25 Apr.</td>
<td>1073</td>
<td>847</td>
<td>−221</td>
</tr>
<tr>
<td>2006</td>
<td>4.9</td>
<td>644</td>
<td>23 Apr.</td>
<td>1003</td>
<td>801</td>
<td>−197</td>
</tr>
<tr>
<td>2007</td>
<td>4.6</td>
<td>699</td>
<td>13 Apr.</td>
<td>1104</td>
<td>857</td>
<td>−241</td>
</tr>
<tr>
<td></td>
<td>Random/systematic uncertainty</td>
<td>40/100</td>
<td>40/100</td>
<td>30/80</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

¹⁾ Data from Finnish Meteorological Institute.
μmol m⁻²(ground) s⁻¹ and the extrapolated daytime respiration 2–3 μmol m⁻² s⁻¹. \( R_{stem} \) was most of the time smaller than 1 μmol m⁻²(ground) s⁻¹. CO₂ efflux from the soil was approximately 0.5 μmol m⁻² s⁻¹ in winter and peaked in July at 5–6 μmol m⁻² s⁻¹, typical summertime fluxes being about 4 μmol m⁻² s⁻¹. The photosynthesis of the ground vegetation could momentarily in spring and in early summer compensate for the CO₂ emitted from the soil, but on a daily basis there was a net efflux of CO₂ from the forest floor all the time.

In winter there was notable photosynthetic CO₂ uptake only during warm spells when temperature rose above 0 °C. At freezing temperatures the rates of stand photosynthesis and aboveground respiration were very low and there was very little diurnal variation in \( \text{NEE}_\text{EC} \). Soil CO₂ efflux, however, continued over the whole winter. Normally only the organic layer was frozen in winter, therefore, root and microbial activity could take place all year round in the mineral soil and \( R_{soil} \) never ceased totally. \( R_{soil} \) thus dominated the ecosystem CO₂ exchange in winter (Fig. 3). At air temperatures below about –5 °C, the CO₂ exchange virtually consisted of \( R_{soil} \) alone. The majority of the stand’s respiratory fluxes originated below the soil surface also during the growing season (Fig. 3). Only during warm spells in spring the proportion of \( R_{soil} \) dropped slightly below 50% of \( R_{ec} \). \( R_{soil} \) contributed to one third and \( R_{stem} \) was in the order of 10% of total respiration.

The EC measurements indicate that the stand takes up CO₂ on a daily basis from approximately mid-April to late August (Fig. 4). In the summer the daily CO₂ balance largely depends on the magnitude of photosynthetic production, which in turn largely follows irradiance. From autumn to early spring the respiratory fluxes dominated the stand CO₂ exchange and the stand was a source of CO₂ to the atmosphere. Net ecosystem exchange from the chambers showed similar seasonality (not shown).
The annual component CO₂ fluxes are summarised in Tables 1 and 2. The annual GPP_EC in 2002–2007 ranged between 974 and 1104 g C m⁻² and Rₑ,EC between 802 and 857 g C m⁻². Year-to-year variation in the annual chamber-based GPP, Rₑ and net CO₂ exchange was greater than in the corresponding EC-based estimates. The annual chamber-based GPP of the trees in 2002–2006 varied between 890 and 990 g C m⁻² a⁻¹ and the predicted canopy GPP between 840 and 1000 g C m⁻² a⁻¹. SPP calculates $R_{\text{shoot}}$ with a fixed temperature response. In the derivation of eddy-covariance-based GPP_EC, on the other hand, the base level of respiration was estimated daily. Comparison of GPP_EC with the predicted GPP thus requires that respiration is estimated in the same way. When chamber-based $R_{\text{shoot}}$ was also used when calculating the predicted GPP, year-to-year variation in the predicted GPP was reduced to about 100 g C m⁻² a⁻¹, the range of the annual $R_{\text{shoot}}$ being from 218 to 282 g C m⁻². Note that this replacement of predicted $R_{\text{shoot}}$ by the chamber-based values did not alter the net CO₂ exchange of the canopy, only the partition-

<table>
<thead>
<tr>
<th>Year</th>
<th>Predicted GPP of trees</th>
<th>Chamber-based GPP of trees</th>
<th>GPP of ground vegetation</th>
<th>$R_{\text{shoot}}$</th>
<th>$R_{\text{stem}}$</th>
<th>$R_{\text{soil}}$</th>
</tr>
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<tbody>
<tr>
<td>2002</td>
<td>968</td>
<td>989</td>
<td>123</td>
<td>245</td>
<td>67</td>
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<tr>
<td>2003</td>
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<td>889</td>
<td>108</td>
<td>260</td>
<td>62</td>
<td>634</td>
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<tr>
<td>2004</td>
<td>889</td>
<td>964</td>
<td>95</td>
<td>218</td>
<td>60</td>
<td>619</td>
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<td>64</td>
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<tr>
<td>2006</td>
<td>875</td>
<td>988</td>
<td>135</td>
<td>246</td>
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<td>100/100</td>
<td>30/30</td>
<td>50/50</td>
<td>15/30</td>
<td>50/100</td>
</tr>
</tbody>
</table>

1) with chamber-based $R_{\text{shoot}}$
ing between GPP and $R_{\text{shoot}}$ was changed, most notably in 2006. Due to the warm summer, the fixed temperature response predicted the highest annual $R_{\text{shoot}}$ of all years (380 g C m$^{-2}$) whereas estimating the respiration directly from the chambers indicated only average $R_{\text{shoot}}$ (247 g C m$^{-2}$ a$^{-1}$) for that year.

Photosynthetic production of the dwarf shrub and moss vegetation was 95–135 g C m$^{-2}$ a$^{-1}$, on average 12% of the GPP of the whole stand. The mosses contributed to about 30% of the cumulative ground vegetation GPP. The annual $R_{\text{soil}}$ was 537–637 g C m$^{-2}$ and the annual $R_{\text{stem}}$ 57–67 g C m$^{-2}$ (Table 2). $R_{\text{soil}}$ in 2006 was among the lowest of the five years of chamber data studied here.

Annually the SMEAR II stand was a net sink of carbon. The net C uptake detected by EC varied between 136 and 241 g C m$^{-2}$ a$^{-1}$ and there was no significant trend over the period. The net C uptake based on chambers varied more, from 41 to 283 g C m$^{-2}$ a$^{-1}$.

**Relationships between the fluxes and environmental factors**

Year-to-year variation in the annual GPP$_{\text{EC}}$, NEE$_{\text{EC}}$ and $R_{\text{EC}}$ could be best explained by the starting date of the growing season (Fig. 5a). The definition of the growing season is somewhat arbitrary but different definitions did not change the general relationship between the start of the growing season and GPP$_{\text{EC}}$ or NEE$_{\text{EC}}$.

Besides the onset of the growing season, no single environmental driving factor could be pointed out to explain the interannual variation in GPP$_{\text{EC}}$, $R_{\text{EC}}$ or NEE$_{\text{EC}}$. The greatest C sequestration occurred in 2007 and 2004 that had rainy and cool summers. On the other hand, the warm and sunny summer and the early commencement of winter in 2002 also led to high C sequestration. The dry summer of 2006 did not affect much the annual NEE although the CO$_{2}$ sink of the stand was lower than typical from approximately mid-July to the end of August. The early summer was warm which partly compensated for the lower late-summer fluxes. Also both GPP and $R_{e}$ declined during the drought which resulted in only a small decrease in NEE.

In general, the interannual variation of GPP$_{\text{EC}}$ and $R_{\text{EC}}$ compensated each other so that GPP$_{\text{EC}}$, $R_{\text{EC}}$ and NEE$_{\text{EC}}$ were all connected with each other (Fig. 5b).

**GPP**

Seasonal courses of the predicted GPP agreed very well with the chamber-based GPP and GPP$_{\text{EC}}$, coefficient of determination ($r^2$) for the daily GPP being 0.90–0.95 in different years. Light-saturated GPP was nearly constant from early June until late August but daily photosynthetic production started to decline in August due to decreasing light and daylight hours. The light-driven diurnal patterns of photosynthesis were superimposed over the temperature-driven seasonal cycle that determines the level of light-saturated photosynthesis.

The decline in photosynthesis during the drought of 2006 was well predicted by the model.
Ecosystem respiration and its partitioning

The respiratory CO$_2$ effluxes were low in winter. At low temperatures the relationship between momentary $R_{\text{stem}}$ and temperature was markedly different from the typical exponential relationship; at about $-5$ °C $R_{\text{stem}}$ abruptly ceased (mean nighttime fluxes are shown in Fig. 7). $R_{\text{shoot}}$ diminished below the detection limit at roughly the same temperature but the temperature response was smoother.

The respiratory fluxes increased steeply in spring. $R_{\text{shoot}}$ and $R_{\text{stem}}$ rose more rapidly and peaked earlier in the summer than $R_{\text{soil}}$ which could be explained by the more rapid rise in air temperature as compared with soil temperature in spring. In autumn, soil temperature declined slowly and the relative contribution of $R_{\text{soil}}$ to total respiration increased towards winter. The seasonal courses of the respiratory effluxes could be explained fairly well with temperature alone. Within one day, respiration also followed temperature. The observed apparent long-term temperature relationships were, however, different from the instantaneous temperature responses. The apparent temperature sensitivity ($Q_{10}$) in $R_{\text{soil}}$ was clearly higher in the annual time scale, approximately 3, than in the momentary fluxes where $Q_{10}$ was 2. $R_{\text{shoot}}$ showed quite different patterns; the instantaneous temperature responses were similar to the long-term response.

The base level of respiration ($R_{10}, r_{10}$) showed seasonal variation, being higher in the growing season than in winter (Fig. 8). In the aboveground CO$_2$ effluxes the peak occurred in late spring whereas the soil CO$_2$ efflux normalised to a standard temperature was at its maximum in late summer. As the base level does not give information on the magnitude of the actual CO$_2$ efflux, we also compared the measured effluxes with predictions with the average apparent temperature responses. Similarly to the base level of respiration, daily $R_{\text{shoot}}$ and $R_{\text{stem}}$ compared with the apparent temperature responses were higher in spring and early summer and smaller in late summer and autumn (Fig. 9). Soil CO$_2$ efflux compared with the apparent temperature response peaked later than the aboveground respiration components, the highest fluxes in comparison with the apparent response were observed in July and August (Fig. 9).

The effect of soil moisture on $R_{\text{soil}}$ could
During the period studied, this occurred very briefly in August 2002 and in September 2003. More clear effects of drought were seen in late summer of 2006 when all respiration components decreased gradually. The decline became obvious in the second half of July and the lowest respiratory fluxes were observed on 16 August. By then, all respiration components had decreased to 50%–70% of the values observed in the beginning of July. \( R_{10} \) and \( r_{10} \) during the drought were also considerably lower than in the moist summer of 2004 (Fig. 8).

The seasonal patterns of the respiration to GPP ratios were similar in all years. The ratios of daily \( R_{stem} \) and \( R_{shoot} \) to GPP were relatively stable from early April through September (Fig. 10) whereas \( R_{soil} \) to GPP increased. The proportions of respiration components from total respiration be seen as peaks in the fluxes and in the base level of respiration after wetting of the soil. During dry spells \( R_{soil} \) normally decreased slightly. Considerable decline in \( R_{soil} \) however, was not observed until volumetric water content in the upper mineral soil dropped below ca. 13%.

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tion also followed similar seasonal patterns in all years (Fig. 3). During the drought in 2006, daily $R_{\text{soil}}$, $R_{\text{stem}}$ and $R_{\text{shoot}}$ to GPP ratios increased somewhat from their typical midsummer values (Fig. 10) but there was little deviation from the general seasonal pattern.

**Uncertainties in deriving GPP and $R_e$ from EC**

We estimated the effect of using different environmental factors (air temperature $T_{\text{air}}$, organic layer temperature $T_{\text{H}}$ and upper mineral soil temperature $T_{\text{A}}$) on the estimated $R_{e,\text{EC}}$ and GPP$_{\text{EC}}$. The coefficient of determination ($r^2$) of the $R_e$ model was in the order of 0.3 when the model was fitted to summertime data and 0.7 when the data from a full year were used. $T_{\text{H}}$ yielded consistently better $r^2$ than the other explanatory factors but the difference was only in the order of 0.05. The range of variation in the annual $R_{e,\text{EC}}$ and GPP$_{\text{EC}}$ was about 7% with different explanatory variables of the $R_e$ model. $R_{e,\text{EC}}$ based on the air temperature was 4% higher than $R_{e,\text{EC}}$ calculated with the organic layer temperature. The mineral soil temperature, on the other hand, gave 3% lower annual $R_{e,\text{EC}}$ and GPP$_{\text{EC}}$ than $T_{\text{H}}$. The relative interannual variation in $R_{e,\text{EC}}$ and GPP$_{\text{EC}}$ was fairly independent of $R_e$ model and its driver but more strongly affected by the time scale of estimating the temperature response of $R_e$. The variation originating from different drivers was reduced somewhat by determining the short-term temperature sensitivity of $R_e$ monthly instead of using a fixed value that overestimates the instantaneous temperature response of $R_e$.

The selection of $R_e$ driver and the accuracy of the estimated temperature sensitivity affected not only the absolute level of the fluxes, but also their diurnal patterns (Fig. 11). Daily minima and maxima occur later in the soil than in the air temperature. The diurnal courses of $R_{e,\text{EC}}$ and, consequently, GPP$_{\text{EC}}$ will therefore depend on the $R_e$ model. Diurnal courses of $R_{e,\text{EC}}$ calculated from $T_{\text{A}}$ and $T_{\text{air}}$ showed the closest agreement with chamber-based $R_e$ (Fig. 11). A corresponding afternoon decrease was seen in GPP$_{\text{EC}}$ when $T_{\text{A}}$ was used as the driving variable, whereas the diurnal courses of GPP$_{\text{EC}}$ derived from $T_{\text{A}}$ and $T_{\text{air}}$ were in better agreement with the chamber-based GPP (Fig. 11).
CO2 exchange of a Scots pine forest

Discussion

Magnitude and partitioning of ecosystem CO2 exchange

The net CO2 exchange, GPP and R from eddy covariance were comparable to other boreal coniferous sites (Luyssaert et al. 2007) and to the EC measurements at the site in earlier years (Markkanen et al. 2001, Kolari et al. 2004). The interannual variability of NEEEC was also similar to other northern forest sites (e.g. Luyssaert et al. 2007, Lagergren et al. 2008). The magnitudes and partitioning of the respiratory CO2 fluxes at SMEAR II were similar to another Scots pine stand in eastern Finland (Wang et al. 2004). In boreal forest ecosystems, Rsoil has been found to contribute to more than half of Re (Widen and Majdi 2001, Wang et al. 2004). Rsoil at SMEAR II stand fell roughly halfway the observed range of 0.38–0.99 in temperate and boreal forests (Janssens et al. 2001). The magnitudes of Rshoot and Rstem were similar to those found in other studies (Acosta et al. 2004, Zha et al. 2007). Davidson et al. (2006) found a distinct pattern for Rsoil and Re with clear minimum in their ratio in the spring. In a transect study in nearby forest ecosystems, Ťupek et al. (2008) found that in some cases the forest floors acted as carbon sinks in spring due to low Rsoil.

Photosynthesis

Year-to-year variation in the annual GPPEC and NEEEC could be best explained by the starting date of the growing season. The length of the growing season has been found to correlate well with NEE across sites (Churkina et al. 2005). Within-site variability in the annual NEE, however, is less clearly related to the growing season length; Lagergren et al. (2008) did not find significant correlation for Hyytiälä nor for other forested sites studied in their paper.
It is obvious that inspection of CO₂ exchange and the environmental driving factors on an annual basis cannot properly reveal the appropriate drivers behind the observed fluxes. Therefore, we should study the within-year variation in the fluxes and in the responses to the environmental drivers to understand the interannual variability in the carbon balance. In spring (April) and in late summer and early autumn (Aug.–Sep.) the magnitude of daily NEE varied a lot which suggests that these periods may be critical for the annual C budgets. The definition of the growing season is bound to temperature. In spring, temperature has a strong effect because there is plenty of light available and low temperature is the limiting factor for photosynthesis (cf. Suni et al. 2003). On the other hand, variations in temperature in late autumn can cause only minor changes in annual GPP because photosynthetic CO₂ uptake is largely limited by low light. The early winter of 2006 was exceptionally warm with mean temperature of 1.3 °C in December as compared with the average of –5.1 °C, yet the additional GPP compared with that of an average December was negligible, about 3 g C m⁻² or 0.3% of the annual GPP.

Despite the good agreement in within-year fluxes (Fig. 6), the predicted GPP could not fully explain the observed interannual variation in GPP EC (Table 1 and 2). Mäkelä et al. (2006) found similar discrepancy in 1997–2001, and suggested that the inability of the model to predict the interannual variation might be due to omission of soil water status. Implementing soil water effects to SPP reduced the predicted annual GPP in 2006 by 50 g C m⁻² and made the predicted GPP a better match to the year-to-year pattern in GPP EC. Year 2004 was an exception; the predicted GPP was clearly lower than GPP EC. The moist conditions in the summer of 2004 may have favoured photosynthesis of trees and ground vegetation despite the slightly lower than average summertime temperature.

The midsummer maximum of light-saturated stand photosynthesis \( P_{\text{e,max}} \) was about 10% lower in 2003 than in the other years studied here and coincided with the low GPP EC and NEE EC observed in that year. Lagergren et al. (2008) found that at three forested sites, including Hytylälä, \( P_{\text{e,max}} \) explained more of the interannual variation in GPP EC and NEE EC than environmental factors or the onset of growing season. The low \( P_{\text{e,max}} \) in 2003 may reflect the conditions in the previous autumn and winter: the autumn of 2002 was very dry and the soil water storage was not replenished as usually. The winter started abruptly and early and the dry soil froze deeper than normally during the winter. This harsh winter may have affected photosynthetic capacity. The similar \( P_{\text{e,max}} \) in 2007 compared to the other years suggests that there was no carry-over effect of drought from the previous summer.

**Respiration**

The respiratory fluxes generally followed seasonal courses similar to their obvious driving temperatures, i.e. air temperature for \( R_{\text{shoot}} \) and \( R_{\text{stem}} \), and soil temperature for \( R_{\text{soil}} \). Below approximately –5 °C the aboveground fluxes diminished, \( R_{\text{stem}} \) very abruptly. Sevanto et al. (2006) observed very large variation in the stem diameter at temperatures below –5 °C that they associated with stem freezing. The freezing also inhibits diffusion of CO₂ out of the stem.

The base level of respiration \( (R_{10}, r_{10}) \) estimated from the aboveground CO₂ effluxes showed higher values in the early growing season than in late summer and in autumn (Fig. 8). There were also consistent deviations from the apparent long-term temperature responses: \( R_{\text{shoot}} \) and \( R_{\text{stem}} \) compared to predictions with the average apparent temperature responses were higher in spring and early summer and smaller in late summer and autumn (years 2004 and 2006 shown in Fig. 9). This could reflect the higher respiratory activity when the trees are recovering from winter dormancy and starting growth. The highest levels of temperature-normalised respiration rate have been found to coincide with the highest rates of stem diameter growth (e.g. Zha et al. 2005). In our study, however, the maxima in the temperature-normalised \( R_{\text{shoot}} \) and \( R_{\text{stem}} \) were observed already in early May whereas the rates of shoot elongation and diameter growth in Scots pine at the site normally peak in early June (Pietarinen et al. 1982). The higher spring and early growing season respiration as compared with that in autumn may also be explained by better availability of sugars.
as substrate for respiration due to higher photosynthetic production and release of carbohydrates from the internal storage pools. The ratios of \( R_{\text{shoot}} \) and \( R_{\text{stem}} \) to GPP were relatively stable over the growing seasons and the observed seasonal cycles in the base level of \( R_{\text{shoot}} \) and \( R_{\text{stem}} \) could as well be explained by stable \( R_{\text{GPP}} \) ratio. Temperature-normalised respiration was high in late spring when low temperatures were combined with relatively high photosynthetic production.

The seasonal patterns of \( R_{\text{soil}} \) coincided with the seasonal courses of temperature in the upper mineral soil and the increase in the relative contribution of \( R_{\text{soil}} \) to \( R_e \) towards autumn could be largely explained by the different seasonal patterns of air and soil temperature. There was also temperature-independent seasonal variation in \( R_{\text{soil}} \): \( \text{CO}_2 \) efflux in standard temperature peaked in August or September (Fig. 8). Possible explanations are the peak in the litterfall that occurs in autumn and the growth of fine roots in trees taking place later than the aboveground growth. It is also probable that some of the observed seasonal variation in \( R_{\text{IO}} \) and \( r_{\text{IO}} \) is caused by shortcomings in the exponential respiration model, despite the addition of a constant term to the \( R_{\text{shoot}} \) model to increase the temperature sensitivity at low temperatures. Values of \( R_{\text{IO}} \) and \( r_{\text{IO}} \) estimated at the same temperature range, however, are directly comparable regardless of the functional form of the model.

The decoupling of respiration from temperature was further demonstrated in the very short dry periods in 2002 and 2003 and especially during the warm summer and the prolonged drought in 2006. The respiration components in 2006 were lower than the predictions solely based on temperature, the difference in the annual \( R_{\text{shoot}} \) was as much as 30%. Part of the decline in \( R_{\text{soil}} \) during the drought can be explained by reduction of microbial decomposition in the dry soil. A large part of the \( \text{CO}_2 \) emanating from the soil originates in roots (Boone et al. 1998, Högberg and Read 2006). Overall the proportion of root respiration in considered to be approximately half of the soil \( \text{CO}_2 \) efflux (e.g. Bhupinderpal-Singh et al. 2003). Girdling study at SMEAR II showed similar partitioning (J. F. J. Korhonen unpubl. data). Root and rhizosphere respiration and root growth are also related to photosynthetic production (Högberg et al. 2001, Ekblad et al. 2005, Knohl et al. 2005, Tang et al. 2005), the contribution of recently produced photosynthesize in soil \( \text{CO}_2 \) efflux at SMEAR II was estimated to be approximately 25% in early summer (Pumpanen et al. 2008). Therefore, the reduction in \( R_{\text{soil}} \) can also be attributed to decreased supply of photosynthates to the root system. The exceptionally warm period in November and December 2006 did not result in as big an increase in \( R_{\text{soil}} \) as the apparent temperature response predicted (Fig. 9), possibly because the supply of photosynthates into the soil had virtually ceased. Also the temperature-normalised respiration stayed low (Fig. 8). The stand was a stronger source of \( \text{CO}_2 \) to the atmosphere than in normal winters mainly due to increased aboveground respiration.

Temperature is generally considered as the major factor controlling respiration (e.g. Lloyd and Taylor 1994) but Lagergren et al. (2008) found that nighttime temperature explained less than 15% of the between-year variation in nighttime \( N_{\text{EC}} \) for July and August. Instead they found a stronger relationship between \( R_e \) and \( P_{\text{e, max}} \), which agrees with the observations of Janssens et al. (2001). The correlations between the annual \( G_{\text{EC}} \), \( R_{\text{EC}} \) and \( N_{\text{EC}} \) in our study support the hypothesis that respiration is dependent on substrate supply as suggested by e.g. Waring et al. (1998). Respiration and NEE are determined not only by the environmental driving factors but also by the availability of photosynthates and demand for energy in the plant tissues. The proportion of autotrophic respiration from GPP should be fairly stable when integrated over long periods of time, respiration being constrained by GPP (e.g. Dewar et al. 1998). A large part of \( \text{CO}_2 \) efflux from heterotrophic respiration originates in prompt utilisation of recently produced photosynthesize, root exudates. Thus, also \( R_e \) would be in long term roughly proportional to GPP although the momentary \( R_e \) to GPP ratio will vary due to storage and delays in the transport of photosynthates.

**Uncertainty in the chamber-based fluxes**

The chamber-based fluxes included uncertainty
at different time scales: more or less constant systematic errors, errors varying from year to year and errors varying seasonally or diurnally (Table 2). The exact magnitudes of systematic errors could not be determined, therefore, the values in Table 2 must be seen as order-of-magnitude estimates.

Only the soil chambers yield fluxes directly as a unit C per m² ground, the rest of the chamber fluxes must be upcaled to the stand level by utilising idealised assumptions on the spatial variation of the physiological properties and the environmental driving factors. On the other hand, the flux component with the most straightforward upcaling procedure \( R_{soil} \) was the most problematic in terms of the accuracy of the flux measurement whereas for \( R_{shoot} \) the situation was the opposite. The integration of photosynthesis from the shoots to the stand was probably the greatest source of more or less time-independent systematic error in the fluxes, the uncertainty being in the order of 10%–15%.

All chamber-based fluxes included sampling error due to the small number of the chambers. The sampling error was especially large in \( R_{soil} \) due to the large spatial variation in below-ground \( \text{CO}_2 \) production. The soil fluxes from the automated chambers were re-scaled using manually measured fluxes but these also had uncertainty of approximately 50 g C m⁻² a⁻¹ based on the standard error of mean from 14 samples. Naturally the manual chamber can yield biased flux estimates, thus, some systematic error remained in \( R_{soil} \). The uncertainty originating from the small number of samples is also demonstrated in the annual chamber-based GPP; its variation from year to year was different from the courses of the predicted GPP and GPP_EC. The random error in the predicted GPP can be considered very small and mainly originate from the measurements of the driving factors.

The growing shoots were poorly represented in \( R_{shoot} \). New needles start expanding in the first half of June when the new shoots have almost reached their full length. Respiration of the new shoots was assumed proportional to needle area, i.e. the respiration of the growing shoots still without needles was omitted. Chamber data on intact shoots from Hyytiälä is scant but from the measurements we have (unpubl. data) we can estimate that the maximum underestimation of \( R_{shoot} \) in early summer was in the order of 20%. The annual growth respiration of the new shoots can be estimated at 25% of the shoot biomass increment (Penning de Vries 1975) which implies a missing respiration component of approximately 30 g C m⁻² a⁻¹. This could be one reason why the chamber-based \( R_e \) consistently matched \( R_{EC} \) in the early growing season whereas in late summer the chambers tended to overestimate \( R_{EC} \). Growth respiration in the other parts of the tree was embedded in the stem and soil chamber measurements.

\( R_{stem} \) was upcaled to the stand by simple multiplication of \( \text{CO}_2 \) efflux per unit stem surface area by the total stem and branch surface area in the stand. The relative uncertainty in the \( R_{stem} \) estimate is high because the partitioning of stem tissues to xylem, phloem and cambium varies within a tree. Vertical profiles of \( \text{CO}_2 \) efflux and local \( \text{CO}_2 \) production are also different because part of the respired \( \text{CO}_2 \) is transported up the stem in xylem sap (Teskey et al. 2008). The absolute uncertainty in the annual \( R_{stem} \), however, is small due to the small contribution (< 10%) of the aboveground woody tissues to \( R_e \).

The integration of the ground vegetation GPP was based on light and temperature only. Especially in the rootless mosses, photosynthetic rate depends a lot on water status (e.g. Skre and Oechel 1981, Williams and Flanagan 1998, Kulmala et al. 2008) which was not taken into account here, so the actual proportion of the ground vegetation GPP may vary considerably over the summer. If we assume that \( P_{max} \) of the ground vegetation decreased proportionally to the photosynthetic efficiency (\( \beta \)) of the Scots pine foliage during the drought in 2006, GPP of the ground vegetation would have been 10%–20% smaller than we estimated. The drought may have affected the ground vegetation even more because the roots are in the topmost layer of the soil that dries out before the deeper soil layers, and the mosses have no means of taking up water from the mineral soil. Roughly 30% of the foliage area in the ground vegetation was deciduous, therefore, the estimation of photosynthetic efficiency from the evergreen trees might overestimate the photosynthetic capacity of ground vegetation in early spring.
and late autumn. The yearly biomass sampling also involved some uncertainty and might have resulted in exaggerated year-to-year variation in GPP. The ground vegetation contributed to about 12% of whole-stand GPP, thus the uncertainty of the forest floor photosynthesis was a mere 4% of the annual stand GPP.

If we consider the sources of error in the component fluxes independent of each other, the uncertainties of the combined annual chamber-based fluxes (GPP and total respiration) will be roughly 20%. Integrating several different types of flux measurements will unavoidably result in larger interannual variation of NEE (poorer precision of annual C budgets) than a standardised direct flux measurement like EC. On average, however, the chambers and EC agreed fairly well and the diurnal and seasonal courses of the chamber-based fluxes serve as a good reference for the EC-based fluxes.

Uncertainty in the EC-based fluxes

The annual EC-based CO₂ exchange is integrated from half-hourly records that have large random errors due to the stochastic nature of turbulence. The random errors, however, diminish in the long term; Richardson et al. (2006) estimated annual uncertainty of approximately 20 g C m⁻² in NEEEC. The accumulated random error from gap-filling is of the same magnitude (Moffat et al. 2007). The small random error suggests that eddy covariance captures the interannual variability in NEE more precisely than upscaling from chambers.

The annual net C uptake determined by EC in 2002–2007 was systematically up to 100 g C m⁻² lower than the biomass increment in trees within any radius between 35 and 195 m from the EC mast (Ilvesniemi et al. 2009). An obvious explanation to the discrepancy would be decomposition of the cutting debris, stumps and roots that were left at the site in the thinning in early 2002. Systematic errors in the fluxes cannot be ruled out either. Rannik et al. (2006) estimated the uncertainty in the annual NEEEC at SMEAR II to be 80 g C m⁻² based on the systematic difference in fluxes observed with two adjacent EC measuring setups. The errors in NEEEC propagate into GPPEC and Rse,EC with similar magnitude. Thus, the precision of EC in detecting year-to-year variation in GPP and Rse is fairly good, in the order of 50 g C m⁻² a⁻¹. The systematic errors in the flux measurement, however, can be larger. This correspondingly decreases the accuracy of GPPEC and Rse,EC, their uncertainties being in the order of 100 g C m⁻² a⁻¹.

Besides the random and systematic errors in the flux measurement itself, the accuracy of EC-based component fluxes depends on the methods used in deriving the fluxes. GPP is usually calculated as the difference between the measured NEEEC and Rse calculated as a function of air or soil temperature or a combination of those, thus the estimated Rse,EC and GPPEC depend on the type of temperature used as the explanatory variable in Rse model. At times air temperature is used as the driver for a statistical reason; it has larger short-term variation than soil temperature which makes determining the temperature sensitivity of Rse more robust. Practice for measuring soil temperature also varies which can confuse analyses of soil-temperature-based flux estimates across different sites (e.g. van Dijk and Dolman 2004). The aboveground respiration is very low at freezing temperatures and the vast majority of CO₂ efflux originates in the soil where temperature and CO₂ production are very stable throughout the winter. In such conditions, explaining Rse with air temperature will result in large diurnal and day-to-day variation in CO₂ efflux. Seasonally this shows up most clearly in spring and summer when the diurnal variation of air temperature is large. The different daily Rse,EC and GPPEC estimates were virtually equal from approximately mid-August when the diurnal amplitude of air temperature was small. The relative contribution of the aboveground respiration was at its maximum in spring and early summer. Correspondingly, Rse in early summer is more strongly correlated with air temperature than in late summer and autumn when Rsoil dominates.

Ideally the explanatory variable of the Rse model should reflect the relative contributions of Rsoil and the aboveground respiration components to Rse. As the proportions of different component fluxes and correspondingly the significance of the different drivers behind Rse
vary seasonally (Davidson et al. 2006, see also Fig. 3), these requirements cannot be fully met by one explanatory variable only. On the other hand, using more than one driver in the $R_e$ model (e.g. Markkanen et al. 2001) may lead to problems in the estimation of the parameter values due to the noisy EC data.

The variation in $R_{\text{EC}}$ and GPP$_{\text{EC}}$ originating from different drivers can be compensated by accurate determination of the short-term temperature sensitivity of $R_e$. Time window in determining the temperature sensitivity must be long enough to capture the temperature response from the noisy EC fluxes, yet so short that the instantaneous temperature response is not confounded by seasonal co-variation in temperature and in the base level of respiration (Reichstein et al. 2005). Especially in ecosystems with strong summertime drought-induced decline in fluxes, the use of long-term fixed temperature sensitivity gives biased $R_{\text{EC}}$ and GPP$_{\text{EC}}$ but for the summer-active boreal stands it may be justified (Reichstein et al. 2005).

**Conclusions**

CO$_2$ efflux from the forest floor dominated the ecosystem respiration for the whole year, but most clearly in winter. Its relative contribution was smallest in late spring and early summer. Annually it contributed to approximately two thirds of total respiration. Respiration of tree foliage and twigs was the second largest respiration component, its relative and absolute contribution being at its biggest in early summer. Stem CO$_2$ efflux was less than 10% of total respiration. Photosynthesis of the ground vegetation was approximately 12% of the stand GPP.

The integrated chamber-based fluxes agreed well with the eddy-covariance fluxes. Even a small number of chambers can represent the whole stand quite well in terms of diurnal and seasonal variation. Determining the absolute level of fluxes, however, is less precise and accurate due to variation among the sample shoots or forest floor plots being measured. Therefore, the uncertainty in annual chamber-based C budgets is greater than in eddy covariance. Selection of the driver for $R_e$ model is important for the accuracy of $R_e$ and GPP estimated from EC. Proper estimation of short-term responses from EC fluxes is also crucial when deriving GPP and $R_e$ from the measured NEE.

The role of temperature as the primary driving factor behind photosynthesis and respiration in the boreal forests has been recognised in several studies and this analysis of multianual time series of ecosystem and component CO$_2$ fluxes agrees with the earlier studies; the seasonal patterns of respiration components can be largely explained by temperature. In some respect the temperature relationships of respiration are indirect and may reflect the seasonal course of photosynthetic production rather than direct temperature response. This can be concluded from the seasonality of the base level of respiration, from the similar decline of respiration components during drought, and from the correlation between the annual GPP$_{\text{EC}}$ and $R_{\text{EC}}$. Studying e.g. the consequences of climate warming by extrapolating fixed temperature responses of respiration may lead to false conclusions on the development of ecosystem C balance in the future.

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**References**


