

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

delayed response to temperature (Pelkonen and Hari 1980, Mäkelä *et al.* 2004).

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 (R_c) 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 R_c . 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 R_c , from the measured NEE (Stoy *et al.* 2006). There is no standard way to estimate GPP and R_c and they are also dependent on each other; a method that yields biased R_c unavoidably results in biased GPP. The systematic errors in determining GPP and R_c 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 R_c 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 β (light-saturated photosynthesis per unit leaf internal CO₂) that varies seasonally. The daily values of β were obtained with two different methods.

In the first method, the daily values of β 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 τ

$$\frac{dS}{dt} = \frac{T - S}{\tau} \quad (1)$$

The values of β were calculated as a sigmoid function of S using parameter values taken from Kolari *et al.* (2007). The values of β 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 β directly from the measured shoot CO₂ exchange. The values of β 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). β 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 β were scaled so as to match the average value of β from 15 June to 15 July for all shoots and years used in this study.

Canopy GPP estimated with the parameter β 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

$$P = \frac{P_{\max} I}{I + b} \quad (2)$$

The photosynthetic parameters, light-saturated rate of photosynthesis (P_{\max}) and curvature b , were determined separately for blueberry, lingonberry, heather (*Calluna vulgaris*), grasses and moss. The seasonal patterns of P_{\max} were previously found to be similar to the photosynthetic efficiency of Scots pine (Kolari *et al.* 2006). Daily values of P_{\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_{\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_{shoot}), CO₂ efflux from the stems and branches (R_{stem}), and CO₂ efflux from the soil (R_{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:

$$R = R_{10} Q_{10}^{(T-10)/10} \quad (3)$$

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):

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

where c_r is a parameter that forces respiration to zero at -5 °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 CO_2 efflux from the soil and not estimated separately. Short-term temperature sensitivity Q_{10} of R_{soil} was determined by selecting rainless 10-day periods from spring, summer and autumn of 2004 and calculating regressions of nighttime soil CO_2 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 CO_2 effluxes were used for deriving an exponential relationship (of the same form as Eq. 3) between temperature and the CO_2 efflux in order to construct a continuous time series of fluxes. Local CO_2 production by respiration inside the stem follows in short term temperature that lags slightly behind air temperature. CO_2 efflux from the stems in turn lags behind the actual CO_2 production because diffusion out of the stem is slow. The stem CO_2 efflux was modelled as a response to temperature T_{stem} that follows air temperature T_{air} with a time constant τ of 4 hours:

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

Note that T_{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 CO_2 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 CO_2 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 CO_2 efflux in 2004–2005.

The obtained rates of CO_2 release per unit needle surface area were multiplied by the total needle area per m^2 ground in the stand. Stem CO_2 effluxes in the stand were calculated by multiplying the efflux per stem surface area by the total stem and branch surface area ($0.5 \text{ m}^2 \text{ m}^{-2}$ 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 CO_2 below the measuring height. The NEE_{EC} was partitioned into $R_{\text{e,EC}}$ and GPP_{EC} . $R_{\text{e,EC}}$ 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 GPP_{EC} directly from the measured NEE_{EC} as

$$\text{GPP}_{\text{EC}} = -\text{NEE}_{\text{EC}} + R_{\text{e,EC}} \quad (6)$$

When NEE_{EC} was missing or rejected, GPP_{EC} was replaced by empirically modelled ecosystem photosynthesis P_e :

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

where I is incident photosynthetically active radiation (PAR), $P_{\text{e,max}}$ the rate of saturated photosynthesis, θ a parameter defining the convexity of the light response curve, and α the initial slope of the curve. The model was parameterised using GPP_{EC} 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 α 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 ($PAR < 300 \mu\text{mol m}^{-2} \text{s}^{-1}$) 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 α 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 α 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} , α and $P_{e,max}$ were re-estimated using the fixed seasonal course of $P_{e,max}/\alpha$. The same values of θ 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 (CO_2 and H_2O) 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 CO_2 fluxes from eddy covariance are summarised in Table 1.

Magnitude and partitioning of ecosystem CO_2 exchange

Correspondingly to the seasonal variation in the environmental factors, the absolute levels and the partitioning of the component CO_2 fluxes

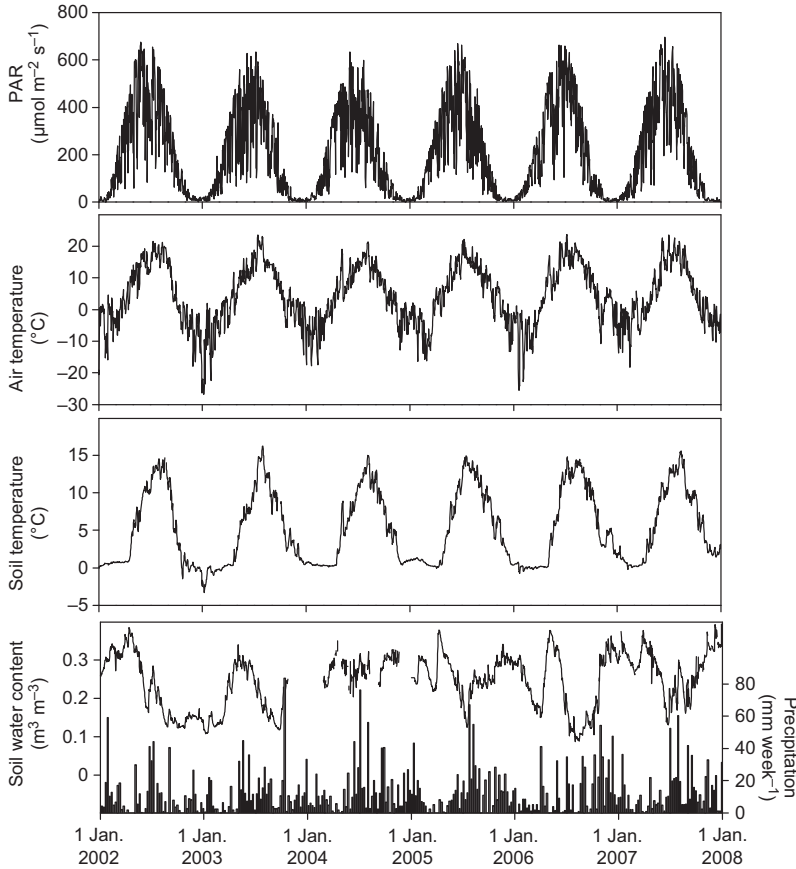


Fig. 1. Daily mean PAR, air temperature, temperature at the depth of 10 cm in the soil, volumetric soil water content (line), and weekly precipitation (bars) at SMEAR II over the years 2002–2007. Precipitation was taken from the weather station of Finnish Meteorological Institute.

varied considerably (Figs. 2 and 3). All CO_2 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

$\mu\text{mol m}^{-2}(\text{ground}) \text{ s}^{-1}$, 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 $2 \mu\text{mol m}^{-2} \text{ s}^{-1}$. 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 CO_2 fluxes with their approximated uncertainties ($\text{g C m}^{-2} \text{ a}^{-1}$) from eddy covariance. The uncertainties of the CO_2 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.

Year	Mean T (°C)	Precipitation ¹⁾ (mm)	Growing season start date	GPP_{EC}	$R_{\text{e,EC}}$	NEE_{EC}
2002	4.2	535	20 Apr.	1084	850	-232
2003	4.1	645	4 May	974	833	-136
2004	4.1	718	16 Apr.	1068	836	-225
2005	4.4	698	25 Apr.	1073	847	-221
2006	4.9	644	23 Apr.	1003	801	-197
2007	4.6	699	13 Apr.	1104	857	-241
Random/systematic uncertainty				40/100	40/100	30/80

¹⁾ Data from Finnish Meteorological Institute.

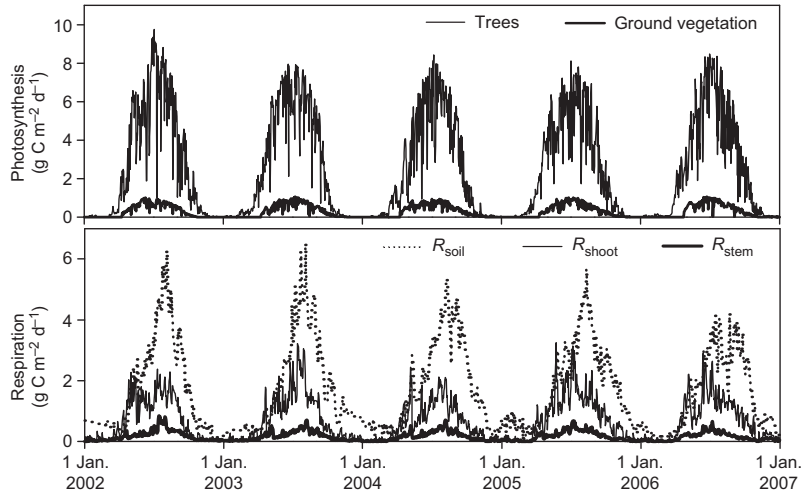


Fig. 2. Seasonal courses of daily photosynthetic production of trees and ground vegetation and respiration components from the chambers over years 2002–2006.

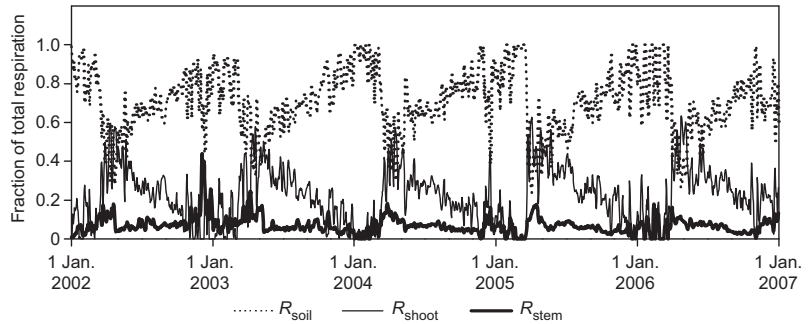


Fig. 3. Relative proportions of daily chamber-based component fluxes over years 2002–2006.

$\mu\text{mol m}^{-2}(\text{ground}) \text{ s}^{-1}$ and the extrapolated daytime respiration $2\text{--}3 \mu\text{mol m}^{-2} \text{ s}^{-1}$. R_{stem} was most of the time smaller than $1 \mu\text{mol m}^{-2}(\text{ground}) \text{ s}^{-1}$. CO_2 efflux from the soil was approximately $0.5 \mu\text{mol m}^{-2} \text{ s}^{-1}$ in winter and peaked in July at $5\text{--}6 \mu\text{mol m}^{-2} \text{ s}^{-1}$, typical summertime fluxes being about $4 \mu\text{mol m}^{-2} \text{ s}^{-1}$. The photosynthesis of the ground vegetation could momentarily in spring and in early summer compensate for the CO_2 emitted from the soil, but on a daily basis there was a net efflux of CO_2 from the forest floor all the time.

In winter there was notable photosynthetic CO_2 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 NEE_{EC} . Soil CO_2 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 CO_2 exchange in winter (Fig. 3). At air temperatures below about -5°C , the CO_2 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_{shoot} 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 CO_2 on a daily basis from approximately mid-April to late August (Fig. 4). In the summer the daily CO_2 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 CO_2 exchange and the stand was a source of CO_2 to the atmosphere. Net ecosystem exchange from the chambers showed similar seasonality (not shown).

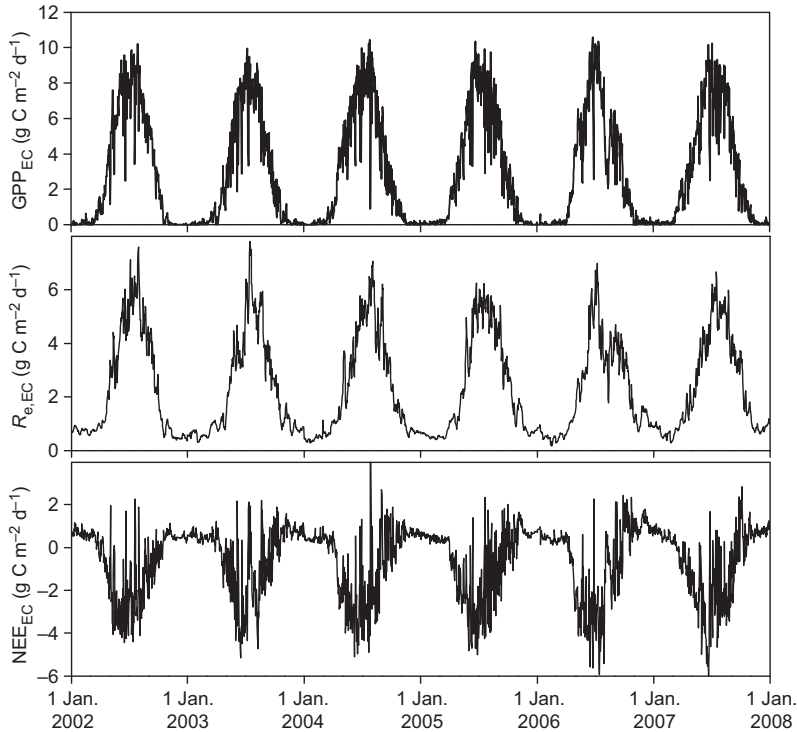


Fig. 4. Seasonal courses of daily photosynthetic production (GPP_{EC}), ecosystem respiration ($R_{e,EC}$) and net ecosystem exchange (NEE_{EC}) from eddy covariance in 2002–2007. Positive NEE indicates loss of carbon from the ecosystem, negative NEE uptake by the ecosystem.

The annual component CO_2 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 $R_{e,EC}$ between 802 and 857 $g\ C\ m^{-2}$. Year-to-year variation in the annual chamber-based GPP, R_e and net CO_2 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_{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_{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_{shoot} being from 218 to 282 $g\ C\ m^{-2}$. Note that this replacement of predicted R_{shoot} by the chamber-based values did not alter the net CO_2 exchange of the canopy, only the partition-

Table 2. Annual upscaled component CO_2 fluxes and their approximated uncertainties ($g\ C\ m^{-2}\ a^{-1}$). The uncertainties of the annual CO_2 budgets are separated into a random component that mainly originates from sampling error, and a systematic component that consists of bias in the flux measurements or in the upscaling procedure.

Year	Predicted GPP of trees ¹⁾	Chamber-based GPP of trees	GPP of ground vegetation	R_{shoot}	R_{stem}	R_{soil}
2002	968	989	123	245	67	602
2003	894	889	108	260	62	634
2004	889	964	95	218	60	619
2005	942	923	125	282	64	637
2006	875	988	135	246	57	537
Random/systematic uncertainty	20/100	100/100	30/30	50/50	15/30	50/100

¹⁾ with chamber-based R_{shoot} .

ing between GPP and R_{shoot} was changed, most notably in 2006. Due to the warm summer, the fixed temperature response predicted the highest annual R_{shoot} of all years (380 g C m⁻²) whereas estimating the respiration directly from the chambers indicated only average R_{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_{soil} was 537–637 g C m⁻² and the annual R_{stem} 57–67 g C m⁻² (Table 2). R_{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_{EC} , NEE_{EC} and $R_{\text{e,EC}}$ 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_{EC} or NEE_{EC} .

Besides the onset of the growing season, no single environmental driving factor could be pointed out to explain the interannual variation in GPP_{EC} , $R_{\text{e,EC}}$ or NEE_{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 CO₂ 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.

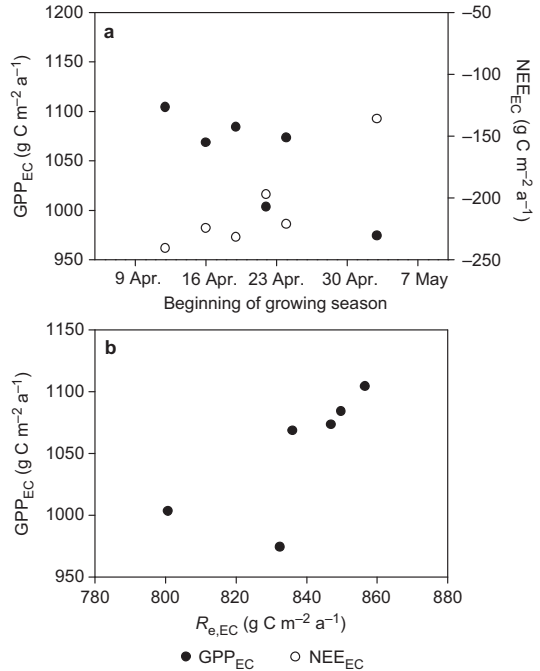


Fig. 5. (a) The annual GPP_{EC} and NEE_{EC} versus the date of the beginning of growing season in 2002–2007, and (b) the annual GPP_{EC} versus ecosystem respiration $R_{\text{e,EC}}$. The beginning of growing season was defined as the date when daily mean temperature reached 5 °C and remained above zero thereafter.

In general, the interannual variation of GPP_{EC} and $R_{\text{e,EC}}$ compensated each other so that GPP_{EC} , $R_{\text{e,EC}}$ and NEE_{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_{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

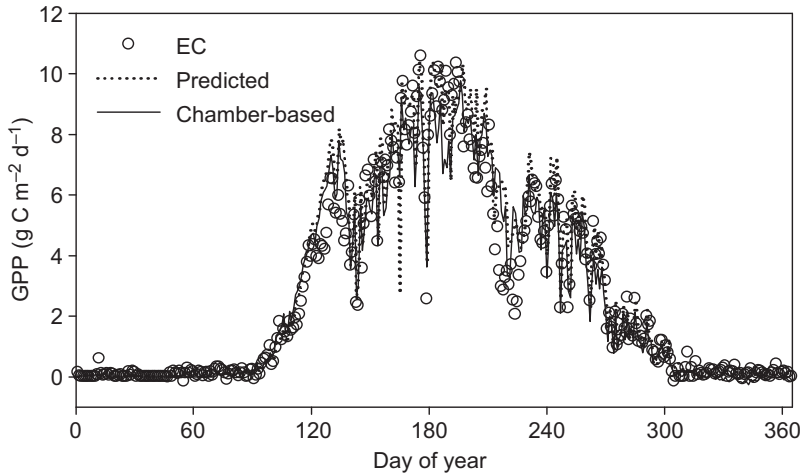


Fig. 6. Daily photosynthetic production (GPP) of the stand during year 2006: GPP extracted from eddy covariance, upscaling directly from chamber measurements, and prediction with SPP.

(Fig. 6). Despite the good agreement in within-year fluxes, the predicted GPP could not fully explain the observed year-to-year variation in GPP_{EC} ; the model failed to predict the high GPP_{EC} in the moist summer of 2004. The lowest annual GPP_{EC} occurred in 2003 which is in line with the short growing season in that year but also the maximum light-saturated GPP_{EC} ($P_{e,max}$ in Eq. 7) was lower than in the other years. $P_{e,max}$ at daily mean VPD range of 0–6 g H₂O m⁻³ during the period of 15 June to 20 July was 18.1 $\mu\text{mol m}^{-2} \text{s}^{-1}$ in 2003 whereas in the other years it was about 20 $\mu\text{mol m}^{-2} \text{s}^{-1}$.

Ecosystem respiration and its partitioning

The respiratory CO₂ effluxes were low in winter. At low temperatures the relationship between momentary R_{stem} and temperature was markedly different from the typical exponential relationship; at about $-5\text{ }^{\circ}\text{C}$ R_{stem} abruptly ceased (mean nighttime fluxes are shown in Fig. 7). R_{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_{shoot} and R_{stem} rose more rapidly and peaked earlier in the summer than R_{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_{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_{soil} was clearly higher in the annual time scale, approximately 3, than in the momentary fluxes where Q_{10} was 2. R_{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 above-ground CO₂ effluxes the peak occurred in late spring whereas the soil CO₂ 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 CO₂ efflux, we also compared the measured effluxes with predictions with the average apparent temperature responses. Similarly to the base level of respiration, daily R_{shoot} and R_{stem} compared with the apparent temperature responses were higher in spring and early summer and smaller in late summer and autumn (Fig. 9). Soil CO₂ 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_{soil} could

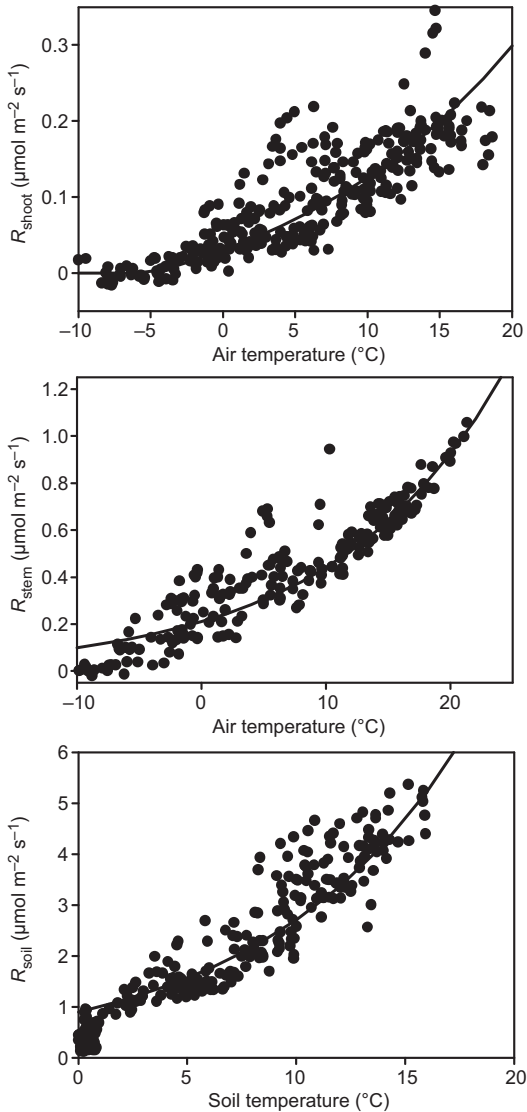


Fig. 7. Relationships between daily mean nighttime temperature and respiration components (R_{shoot} , R_{stem} , R_{soil}) upscaled from the chambers in 2004. The data consist of daily averaged nighttime fluxes only and thus do not involve extrapolation to daytime. Note that R_{shoot} is given in unit CO₂ per m² all-sided needle area and R_{stem} per m² bark surface area instead of ground area. The lines represent the temperature response functions (Eqs. 3 and 4) fitted to the whole-year data.

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

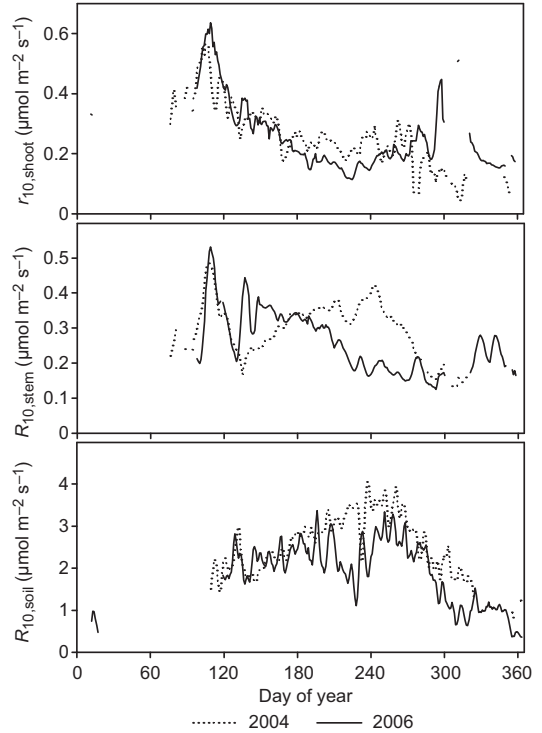


Fig. 8. The base level of respiration (R_{10} , r_{10}) estimated daily from the chambers in 2004 and in 2006. Days when the daily mean air temperature was below zero (R_{shoot} , R_{stem}) or the temperature in the organic layer was < 0.5 °C (R_{soil}) were excluded because the relative uncertainty of the base level of respiration in freezing temperatures is high.

in the upper mineral soil dropped below ca. 13%. 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 respira-

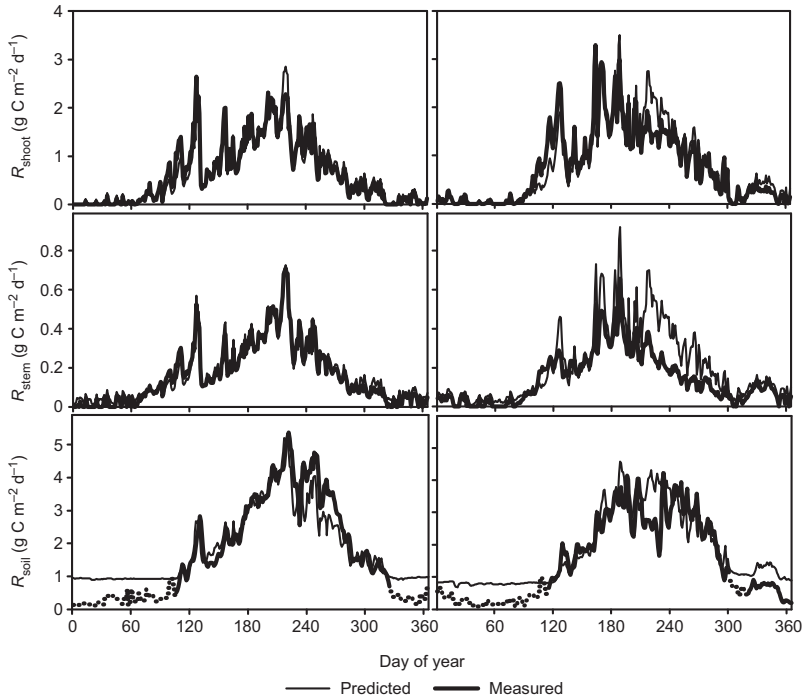


Fig. 9. Seasonal patterns of measured respiration components (R_{shoot} , R_{stem} , R_{soil}) and corresponding predictions with fixed apparent temperature responses in 2004 and 2006. The apparent temperature responses were parameterised using component CO_2 fluxes from years 2002–2004. Dotted parts in the graphs of measured R_{soil} indicate when the ground was covered by snow.

tion also followed similar seasonal patterns in all years (Fig. 3). During the drought in 2006, daily R_{soil} , R_{stem} and R_{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_{air} , organic layer temperature T_{H} and upper mineral soil temperature T_{A}) on the estimated $R_{e,EC}$ and GPP_{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_{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 $R_{e,EC}$ and GPP_{EC} was about 7% with different explanatory variables of the R_e model. $R_{e,EC}$ based on the air temperature was 4% higher than $R_{e,EC}$ calculated with the organic layer temperature.

The mineral soil temperature, on the other hand, gave 3% lower annual $R_{e,EC}$ and GPP_{EC} than T_{H} . The relative interannual variation in $R_{e,EC}$ and GPP_{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 $R_{e,EC}$ and, consequently, GPP_{EC} will therefore depend on the R_e model. Diurnal courses of $R_{e,EC}$ calculated from T_{H} and T_{air} showed the closest agreement with chamber-based R_e (Fig. 11). A corresponding afternoon decrease was seen in GPP_{EC} when T_{A} was used as the driving variable, whereas the diurnal courses of GPP_{EC} derived from T_{H} and T_{air} were in better agreement with the chamber-based GPP (Fig. 11).

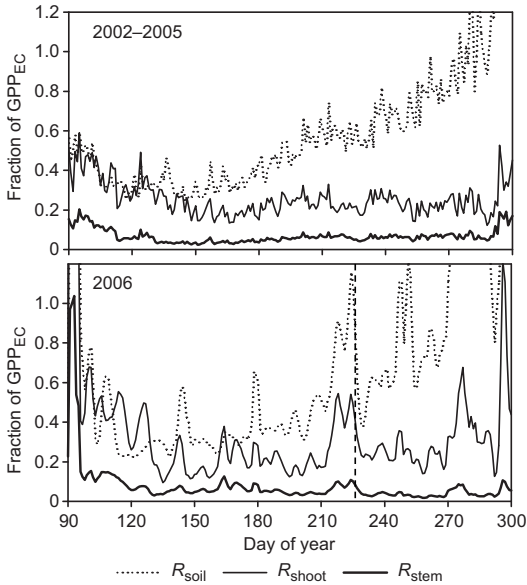


Fig. 10. Daily (running mean of three days) proportions of R_{soil} , R_{shoot} and R_{stem} from GPP_{EC} in 2002–2005 and in the dry year 2006. A vertical dashed line indicates when the drought in 2006 ended.

Discussion

Magnitude and partitioning of ecosystem CO₂ exchange

The net CO₂ exchange, GPP and R_e 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 NEE_{EC} 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, R_{soil} has been found to contribute to more than half of R_e (Widen and Majdi 2001, Wang *et al.* 2004). R_{soil} 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 R_{shoot} and R_{stem} 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 R_{soil} and R_e with clear

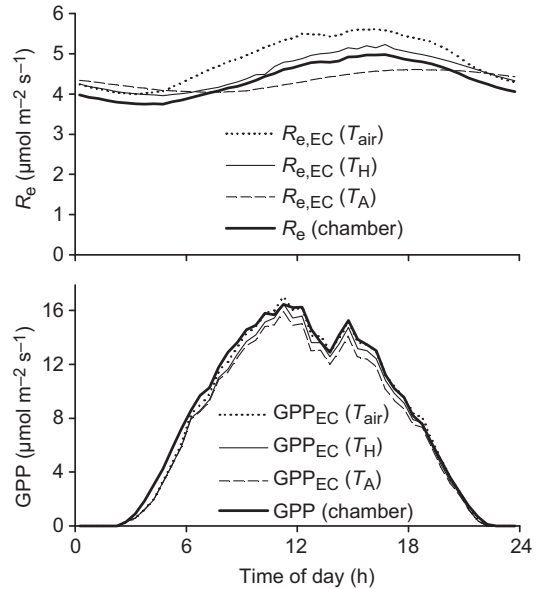


Fig. 11. Diurnal patterns of chamber-based R_e and GPP in comparison with $R_{e,\text{EC}}$ and GPP_{EC} calculated using different explanatory factors for the R_e model. The diurnal patterns were averaged for 15 June–15 July 2004. The sensitivity of $R_{e,\text{EC}}$ to each type of temperature was first estimated from night-time EC fluxes in June and July. Light-saturated stand GPP ($P_{e,\text{max}}$) and the base level of R_e (R_{10}) were then estimated daily in a moving time window of nine days. $R_{e,\text{EC}}(T_{\text{air}})$ and $GPP_{\text{EC}}(T_{\text{air}})$ refer to air temperature as the explanatory factor, $R_{e,\text{EC}}(T_{\text{H}})$ and $GPP_{\text{EC}}(T_{\text{H}})$ to the organic layer temperature, and $R_{e,\text{EC}}(T_{\text{A}})$ and $GPP_{\text{EC}}(T_{\text{A}})$ to the temperature at the depth of 5 cm from the mineral soil surface.

minimum in their ratio in the spring. In a transect study in nearby forest ecosystems, Ľupek *et al.* (2008) found that in some cases the forest floors acted as carbon sinks in spring due to low R_{soil} .

Photosynthesis

Year-to-year variation in the annual GPP_{EC} and NEE_{EC} 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 ($P_{e,max}$) 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 Hyttiälä, $P_{e,max}$ explained more of the interannual variation in GPP_{EC} and NEE_{EC} than

environmental factors or the onset of growing season. The low $P_{e,max}$ 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 $P_{e,max}$ 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_{shoot} and R_{stem} , and soil temperature for R_{soil} . Below approximately –5 °C the aboveground fluxes diminished, R_{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_{shoot} and R_{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_{shoot} and R_{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_{shoot} and R_{stem} to GPP were relatively stable over the growing seasons and the observed seasonal cycles in the base level of R_{shoot} and R_{stem} could as well be explained by stable R/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_{soil} coincided with the seasonal courses of temperature in the upper mineral soil and the increase in the relative contribution of R_{soil} to R_{c} 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_{soil} ; CO₂ 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_{10} and r_{10} is caused by shortcomings in the exponential respiration model, despite the addition of a constant term to the R_{shoot} model to increase the temperature sensitivity at low temperatures. Values of R_{10} and r_{10} 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_{shoot} was as much as 30%. Part of the decline in R_{soil} during the drought can be explained by reduction of microbial decomposition in the dry soil. A large part of the CO₂ emanating from the soil originates in roots (Boone *et al.* 1998, Högberg and Read 2006). Overall the proportion of root respiration is considered to be approximately half of the soil CO₂ 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 photosynthate in soil CO₂ efflux at SMEAR II was estimated to be approximately 25% in early summer (Pumpanen *et al.* 2008). Therefore, the reduction in R_{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_{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 CO₂ 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 NEE_{EC} for July and August. Instead they found a stronger relationship between R_{c} and $P_{\text{e,max}}$, which agrees with the observations of Janssens *et al.* (2001). The correlations between the annual GPP_{EC}, $R_{\text{e,EC}}$ and NEE_{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 CO₂ efflux from heterotrophic respiration originates in prompt utilisation of recently produced photosynthate, root exudates. Thus, also R_{c} would be in long term roughly proportional to GPP although the momentary R_{c} 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 upscaled 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 upscaling 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 CO₂ 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_c consistently matched $R_{c,EC}$ in the early growing season whereas in late summer the chambers tended to overestimate $R_{c,EC}$. Growth respiration in the other parts of the tree was embedded in the stem and soil chamber measurements.

R_{stem} was upscaled to the stand by simple multiplication of CO₂ 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 CO₂ efflux and local CO₂ production are also different because part of the respired CO₂ 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_c .

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 (β) 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 NEE_{EC}. 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 NEE_{EC} 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 NEE_{EC} propagate

into GPP_{EC} and R_{e,EC} with similar magnitude. Thus, the precision of EC in detecting year-to-year variation in GPP and R_e 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 GPP_{EC} and R_{e,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 NEE_{EC} and R_e calculated as a function of air or soil temperature or a combination of those, thus the estimated R_{e,EC} and GPP_{EC} depend on the type of temperature used as the explanatory variable in R_e 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 R_e 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 R_e 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 R_{e,EC} and GPP_{EC} 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, R_e in early summer is more strongly correlated with air temperature than in late summer and autumn when R_{soil} dominates.

Ideally the explanatory variable of the R_e model should reflect the relative contributions of R_{soil} and the aboveground respiration components to R_e. As the proportions of different component fluxes and correspondingly the significance of the different drivers behind R_e

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 $R_{e,EC}$ and GPP_{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 $R_{e,EC}$ and GPP_{EC} but for the summer-active boreal stands it may be justified (Reichstein *et al.* 2005).

Conclusions

CO₂ 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 CO₂ 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 CO₂ 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_{EC} and $R_{e,EC}$. 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

- Acosta M., Pavelka M., Pokorný R., Janouš D. & Marek M.V. 2007. Seasonal variation in CO₂ efflux of stems and branches of Norway spruce. *Ann. Bot.* 101: 311–317.
- Altimir N., Vesala T., Keronen P., Kulmala M. & Hari P. 2002. Methodology for direct field measurements of ozone flux to foliage with shoot chambers. *Atmos. Environ.* 36: 19–29.
- Atkin O.K. & Tjoelker M.G. 2003. Thermal acclimation and the dynamic response of plant respiration to temperature. *Trends Plant Sci.* 8: 343–351
- Aubinet M., Grelle A., Ibrom A., Rannik Ü., Moncrieff J., Foken T., Kowalski A., Martin P.H., Berbigier P., Bernhofer C., Clement R., Elbers J.A., Granier A., Grünwald T., Morgenstern K., Pilegaard K., Rebmann C., Snijders W., Valentini R. & Vesala T. 2000. Estimates of the annual net carbon and water exchange of forest: the EUROFLUX methodology. *Adv. Ecol. Res.* 30: 112–175.

- Ball J.T., Woodrow I.E. & Berry J.A. 1987. A model predicting stomatal conductance and its contribution to the control of photosynthesis under different environmental conditions. In: Biggins J. (ed.), *Progress in photosynthesis research*, Martinus Nijhoff, Dordrecht, pp. 221–224.
- Berninger F., Mäkelä A. & Hari P. 1996. Optimal control of gas exchange during drought: empirical evidence. *Ann. Bot.* 77: 469–476.
- Bhupinderpal-Singh N.A., Nordgren A., Ottosson-Löfvenius M., Högberg M., Mellander P. & Högberg P. 2003. Tree root and soil heterotrophic respiration as revealed by girdling of boreal Scots pine forest: extending observations beyond the first year. *Plant Cell Environ.* 26: 1287–1296.
- Boone R.D., Nadelhoffer K.J., Canary J.D. & Kaye J.P. 1998. Roots exert a strong influence on the temperature sensitivity of soil respiration. *Nature* 396: 570–572.
- Churkina G., Schimel D., Braswell B.H. & Xiao X. 2005. Spatial analysis of growing season length control over net ecosystem exchange. *Global Change Biol.* 11: 1777–1787.
- Davidson E.A., Belk E. & Boone R.D. 1998. Soil water content and temperature as independent or confounded factors controlling soil respiration in a temperate mixed hardwood forest. *Global Change Biol.* 4: 217–227.
- Davidson E.A., Richardson A.D., Savage K.E. & Hollinger D.Y. 2006. A distinct seasonal pattern of the ratio of soil respiration to total ecosystem respiration in a spruce-dominated temperate forest. *Global Change Biol.* 12: 230–239.
- Dewar R.C., Medlyn B.E. & McMurtrie R.E. 1998. A mechanistic analysis of light and carbon use efficiencies. *Plant Cell Environ.* 21: 573–588.
- Duursma R., Kolari P., Perämäki M., Nikinmaa E., Hari P., Delzon S., Loustau D., Ilvesniemi H., Pumpanen J. & Mäkelä A. 2007. Predicting the decline in daily maximum transpiration rate of two pine stands during drought based on constant minimum leaf water potential and plant hydraulic conductance. *Tree Phys.* 28: 265–276.
- Ekblad A., Boström B., Holm A. & Comstedt D. 2005. Forest soil respiration rate and $\delta^{13}\text{C}$ is regulated by recent aboveground weather conditions. *Oecologia* 143: 136–142.
- Falge E., Baldocchi D., Olson R.J., Anthoni P., Aubinet M., Bernhofer C., Burba G., Ceulemans R., Clement R., Dolman H., Granier A., Gross P., Grünwald T., Hollinger D., Jensen N.-O., Katul G., Keronen P., Kowalski A., Ta Lai C., Law B.E., Meyers T., Moncrieff J., Moors E., Munger J.W., Pilegaard K., Rannik Ü., Rebmann C., Suyker A., Tenhunen J., Tu K., Verma S., Vesala T., Wilson K. & Wofsy S. 2001. Gap filling strategies for defensible annual sums of net ecosystem exchange. *Agric. For. Meteorol.* 107: 43–69.
- FAO-Unesco 1990. *Soil map of the world: Revised legend*. World Soil Resources Report 60, FAO, Rome.
- Farquhar G.D. & von Caemmerer S. 1982. Modelling of photosynthetic response to environmental conditions. In: Lange O.L., Nobel P.S., Osmond C.B. & Ziegler H. (eds.), *Physiological plant ecology. II. Water relations and carbon assimilation*, Encyclopaedia of Plant Physiology 12B, Springer Verlag, Berlin, pp. 159–174.
- Gifford R.M. 2003. Plant respiration in productivity models: conceptualization, representation and issues for global terrestrial carbon-cycle research. *Funct. Plant Biol.* 30: 171–186.
- Hari P., Keronen P., Bäck J., Altimir N., Linkosalo T., Pohja T., Kulmala M. & Vesala T. 1999. An improvement of the method for calibrating measurements of photosynthetic CO₂ flux. *Plant Cell Environ.* 22: 1297–1301.
- Hari P. & Kulmala M. 2005. Station for Measuring Ecosystem–Atmosphere Relations (SMEAR II). *Boreal Env. Res.* 10: 315–322.
- Hari P., Mäkelä A., Korpilahti E. & Holmberg M. 1986. Optimal control of gas exchange. *Tree Phys.* 2: 169–175.
- Högberg P., Nordgren A., Buchmann N., Taylor A.F.S., Ekblad A., Högberg M.N., Nyberg G., Ottosson-Löfvenius M. & Read D.J. 2001. Large-scale forest girdling shows that current photosynthesis drives soil respiration. *Nature* 411: 789–792.
- Högberg P. & Read D.J. 2006. Towards a more plant physiological perspective on soil ecology. *Trends Ecol. Evol.* 21: 548–554.
- Ilvesniemi H., Levula J., Ojansuu R., Kolari P., Kulmala L., Pumpanen J., Launiainen S., Vesala T. & Nikinmaa E. 2009. Long-term measurements of the carbon balance of a boreal Scots pine dominated forest ecosystem. *Boreal Env. Res.* 14: 731–753.
- Janssens I.A., Lankreijer H., Matteucci G., Kowalski A.S., Buchmann N., Epron D., Pilegaard K., Kutsch W., Longdoz B., Grünwald T., Montagnani L., Dore S., Rebmann C., Moors E.J., Grelle A., Rannik Ü., Morgenstern K., Oltchev S., Clement R., Gudmundsson J., Minerbi S., Berbigier P., Ibrom A., Moncrieff J., Aubinet M., Bernhofer C., Jensen N.O., Vesala T., Granier A., Schulze E.D., Lindroth A., Dolman A. J., Jarvis P.G., Ceulemans R. & Valentini R. 2001. Productivity overshadows temperature in determining soil and ecosystem respiration across European forests. *Global Change Biol.* 7: 269–278.
- Knohl A., Werner R.A., Brand W.A. & Buchmann N. 2005. Short-term variations in $\delta^{13}\text{C}$ of ecosystem respiration reveals link between assimilation and respiration in a deciduous forest. *Oecologia* 142: 70–82.
- Kolari P., Lappalainen H.K., Hänninen H. & Hari P. 2007. Relationship between temperature and the seasonal course of photosynthesis in Scots pine at northern timberline and in southern boreal zone. *Tellus* 59B: 542–552.
- Kolari P., Pumpanen J., Kulmala L., Ilvesniemi H., Nikinmaa E., Grönholm T. & Hari P. 2006. Forest floor vegetation plays an important role in photosynthetic production of boreal forests. *For. Ecol. Manage.* 221: 241–248.
- Kolari P., Pumpanen J., Rannik Ü., Ilvesniemi H., Hari P. & Berninger F. 2004. Carbon balance of different aged Scots pine forests in southern Finland. *Global Change Biol.* 10: 1106–1119.
- Kulmala L., Launiainen S., Pumpanen J., Lankreijer H., Lindroth A., Hari P. & Vesala T. 2008. H₂O and CO₂ fluxes at the floor of a boreal pine forest. *Tellus* 60B: 167–178.

- Lagergren F., Lindroth A., Dellwik E., Ibrom A., Lankreijer H., Launiainen S., Mölder M., Kolari P., Pilegaard K. & Vesala T. 2008. Biophysical controls on CO₂ fluxes of three Northern forest based on long-term eddy covariance data. *Tellus* 60B: 143–152.
- Lloyd J. & Taylor J.A. 1994. On the temperature dependence of soil respiration. *Funct. Ecol.* 8: 315–323.
- Luyssaert S., Inglima I., Jung M., Richardson A.D., Reichstein M., Papale D., Piao S.L., Schulze E.-D., Wingate L., Matteucci G., Aragao L., Aubinet M., Beer C., Bernhofer C., Black K.G., Bonal D., Bonnefond J.-M., Chambers J., Ciais P., Cook B., Davis K.J., Dolman A.J., Gielen B., Goulden M., Grace J., Granier A., Grelle A., Griffis T., Grünwald T., Guidolotti G., Hanson P.J., Harding R., Hollinger D.Y., Hutrya L.R., Kolari P., Kruijt B., Kutsch W., Lagergren F., Laurila T., Law B.E., Le Maire G., Lindroth A., Loustau D., Malhi Y., Mateus J., Migliavacca M., Misson L., Montagnani L., Moncrieff J., Moors E., Munger J.W., Nikinmaa E., Ollinger S.V., Pita G., Rebmann C., Rouspard O., Saigusa N., Sanz M.J., Seufert G., Sierra C., Smith M.L., Tang J., Valentini R., Vesala T. & Janssens I.A. 2007. CO₂ balance of boreal, temperate and tropical forests derived from a global database. *Global Change Biol.* 13: 1–29.
- Markkanen T., Rannik Ü., Keronen P., Suni T. & Vesala T. 2001. Eddy covariance fluxes over a boreal Scots pine forest. *Boreal Env. Res.* 6: 65–78.
- Mecke M., Westman C.J. & Ilvesniemi H. 2002. Water retention capacity in coarse podzol profiles predicted from measured soil properties. *Soil Sci. Soc. Am. J.* 66: 1–11.
- Moffat A.M., Papale D., Reichstein M., Hollinger D.Y., Richardson A.D., Barr A.G., Beckstein C., Braswell B.H., Churkina G., Desai A.R., Falge E., Gove J.H., Heimann M., Hui D.F., Jarvis A.J., Kattge J., Noormets A. & Stauch V.J. 2007. Comprehensive comparison of gap-filling techniques for eddy covariance net carbon fluxes. *Agric. For. Meteorol.* 147: 209–232.
- Mäkelä A., Hari P., Berninger F., Hänninen H. & Nikinmaa E. 2004. Acclimation of photosynthetic capacity in Scots pine to the annual cycle temperature. *Tree Phys.* 24: 369–378.
- Mäkelä A., Kolari P., Karimäki J., Nikinmaa E., Perämäki M. & Hari P. 2006. Modelling five years of weather-driven variation of GPP in a boreal forest. *Agric. For. Meteorol.* 139: 382–398.
- Palmroth S. & Hari P. 2001. Evaluation of the importance of acclimation of needle structure, photosynthesis, and respiration to available photosynthetically active radiation in a Scots pine canopy. *Can. J. For. Res.* 31: 1235–1243.
- Pelkonen P. & Hari P. 1980. The dependence of the spring-time recovery of CO₂ uptake in Scots pine on temperature and internal factors. *Flora* 169: 398–404.
- Penning de Vries F.W.T. 1975. The costs of maintenance processes in plant cells. *Ann. Bot.* 39: 77–92.
- Pietarinen I., Kanninen M., Hari P. & Kellomäki S. 1982. A simulation model for daily growth of shoots, needles and stem diameter in Scots pine trees. *For. Sci.* 28: 573–581.
- Pumpanen J., Ilvesniemi H. & Hari P. 2003a. A process-based model for predicting soil carbon dioxide efflux and concentration. *Soil Sci. Soc. Am. J.* 67: 402–413.
- Pumpanen J., Ilvesniemi H., Perämäki M. & Hari P. 2003b. Seasonal patterns of soil CO₂ efflux and soil air CO₂ concentration in a Scots pine forest: comparison of two chamber techniques. *Global Change Biol.* 9: 371–382.
- Pumpanen J., Ilvesniemi H., Keronen P., Nissinen A., Pohja T., Vesala T. & Hari P. 2001. An open chamber system for measuring soil surface CO₂ efflux: analysis of error sources related to the chamber system. *J. Geophys. Res.* 106 (D8): 7985–7992.
- Pumpanen J., Ilvesniemi H., Kulmala L., Siivola E., Laakso H., Kolari P., Helenelund C., Laakso M., Uusimaa M. & Hari P. 2008. Respiration in boreal forest soil as determined from carbon dioxide concentration profile. *Soil Sci. Soc. Am. J.* 72: 1187–1196.
- Pumpanen J., Kolari P., Ilvesniemi H., Minkinen K., Vesala T., Niinistö S., Lohila A., Larmola T., Morero M., Pihlatie M., Janssens I., Yuste J.C., Grünzweig J.M., Reth S., Subke J.A., Savage K., Kutsch W., Ostregg G., Ziegler W., Anthoni P., Lindroth A. & Hari P. 2004. Comparison of different chamber techniques for measuring soil CO₂ efflux. *Agric. For. Meteorol.* 123: 159–176.
- Rannik Ü. 1998. On the surface layer similarity at a complex forest site. *J. Geophys. Res.* 103: 8685–8697.
- Rannik Ü., Kolari P., Vesala T. & Hari P. 2006. Uncertainties in measurement and modelling of net ecosystem exchange of a forest. *Agric. For. Meteorol.* 138: 244–257.
- Reichstein M., Falge E., Baldocchi D., Papale D., Aubinet M., Berbigier P., Bernhofer C., Buchmann N., Gilmanov T., Granier A., Grünwald T., Havrankova K., Ilvesniemi H., Janous D., Knohl A., Laurila T., Lohila A., Loustau D., Matteucci G., Meyers T., Miglietta F., Ourcival J.M., Pumpanen J., Rambal S., Rotenberg E., Sanz M., Tenhunen J., Seufert G., Vaccari F., Vesala T., Yakir D. & Valentini R. 2005. On the separation of net ecosystem exchange into assimilation and ecosystem respiration: review and improved algorithm. *Global Change Biol.* 11: 1424–1439.
- Reichstein M., Papale D., Valentini R., Aubinet M., Bernhofer C., Knohl A., Laurila T., Lindroth A., Moors E., Pilegaard K. & Seufert G. 2007. Determinants of terrestrial ecosystem carbon balance inferred from European eddy covariance flux sites. *Geophys. Res. Lett.* 34: L01402, doi:10.1029/2006GL027880.
- Richardson A.D., Hollinger D.Y., Davis K.J., Flanagan L.B., Katul G.G., Stoy P.C., Verma S.B. & Wofsy S.C. 2006. A multi-site analysis of random error in tower-based measurements of carbon and energy fluxes. *Agric. For. Meteorol.* 136: 1–18.
- Ryan M.G. & Law B.E. 2005. Interpreting, measuring and modelling soil respiration. *Biogeochemistry* 73: 3–27.
- Sevanto S., Suni T., Pumpanen J., Grönholm T., Kolari P., Nikinmaa E., Hari P. & Vesala T. 2006. Wintertime photosynthesis and water uptake in a boreal forest. *Tree Phys.* 26: 749–757.
- Sievänen R., Nikinmaa E., Nygren P., Ozier-Lafontaine H., Perttunen J. & Hakula H. 2000. Components of functional-structural tree models. *Ann. For. Sci.* 57: 399–412.
- Skopp J., Jawsom M.D. & Doran J.W. 1990. Steady-state aerobic microbial activity as a function of soil water

- content. *Soil Sci. Soc. Am. J.* 54: 1619–1625.
- Skre O. & Oechel W. 1981. Moss functioning in different taiga ecosystems in interior Alaska. I. Seasonal, phenotypic, and drought effects on photosynthesis and response patterns. *Oecologia* 48: 50–59.
- Stenberg P. 1996. Simulations of the effects of shoot structure and orientation on vertical gradients in intercepted light by conifer canopies. *Tree Phys.* 16: 99–108.
- Stoy P.C., Katul G.G., Siqueira M.B.S., Juang J.-Y., Novick K.A. & Oren R. 2006. An evaluation of methods for partitioning eddy-covariance-measured net ecosystem exchange into photosynthesis and respiration. *Agric. For. Meteorol.* 141: 2–18.
- Suni T., Berninger F., Vesala T., Markkanen T., Hari P., Mäkelä A., Ilvesniemi H., Hänninen H., Nikinmaa E., Huttula T., Laurila T., Aurela M., Grelle A., Lindroth A., Arneth A., Shibistova O. & Lloyd J. 2003. Air temperature triggers the recovery of evergreen boreal forest photosynthesis in spring. *Global Change Biol.* 9: 1410–1426.
- Tang J., Misson L., Gershenson A., Cheng W. & Goldstein A. 2005. Continuous measurements of soil respiration with and without roots in a ponderosa pine plantation in the Sierra Nevada Mountains. *Agric. For. Meteorol.* 132: 212–227.
- Teskey R.O., Saveyn A., Steppe K. & McGuire M.A. 2008. Origin, fate and significance of CO₂ in tree stems. *New Phytol.* 177: 17–32.
- Župek B., Minkkinen K., Kolari P., Starr M., Chan T., Alm J., Vesala T., Laine J. & Nikinmaa E. 2007. Forest floor versus ecosystem CO₂ exchange along boreal ecotone between upland forest and lowland mire. *Tellus* 60B: 153–166.
- Van Dijk A.I.J.M. & Dolman A.J. 2004. Estimates of CO₂ uptake and release among European forests based on eddy covariance data. *Global Change Biol.* 10: 1445–1459.
- Vesala T., Suni T., Rannik Ü., Keronen P., Markkanen T., Sevanto S., Grönholm T., Smolander S., Kulmala M., Ilvesniemi H., Ojansuu R., Uotila A., Levula J., Mäkelä A., Pumpanen J., Kolari P., Kulmala L., Altimir N., Berninger F., Nikinmaa E. & Hari P. 2005. Effect of thinning on surface fluxes in a boreal forest. *Global Biogeochem. Cycles* 19, GB2001, doi:10.1029/2004GB002316.
- Wang K.-Y., Kellomäki S., Zha T.S. & Peltola H. 2004. Component carbon fluxes and their contribution to ecosystem carbon exchange in a pine forest: an assessment based on eddy covariance measurements and an integrated model. *Tree Phys.* 24: 19–34.
- Waring R.H., Landsberg J.J. & Williams M. 1998. Net primary production of forests: a constant fraction of gross primary production? *Tree Phys.* 18: 129–134.
- Widén B. & Majdi H. 2001. Soil CO₂ efflux and root respiration at three sites in a mixed pine and spruce forest: seasonal and diurnal variation. *Can. J. For. Res.* 31: 786–796.
- Williams T.G. & Flanagan L.B. 1998. Measuring and modelling environmental influences on photosynthetic gas exchange in *Sphagnum* and *Pleurozium*. *Plant Cell Environ.* 21: 555–564.
- Zha T., Kellomäki S., Wang K.-Y. & Ryyppö A. 2005. Respiratory responses of Scots pine stems to 5 years of exposure to elevated CO₂ concentration and temperature. *Tree Phys.* 25: 49–56.
- Zha T., Xing T., Wang K.-Y., Kellomäki S. & Barr A.G. 2007. Total and component carbon fluxes of a Scots pine ecosystem from chamber measurements and eddy covariance. *Ann. Bot.* 99: 345–353.