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Autumn warming and carbon balance of a boreal Scots pine forest in Southern Finland

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Abstract

We analyzed the dynamics of carbon balance components: gross primary production (GPP) and total ecosystem respiration (TER), of a boreal Scots pine forest in Southern Finland. Our aim was to study how these dynamics are related to different environmental conditions and how they affect the inter-annual variation in the carbon balance in autumn (September–December). We used standard micrometeorological data and CO₂ exchange measurements collected by the eddy covariance (EC) technique over 11 years. The intra-annual relationships between the carbon balance components and the environmental factors were studied by the correlation analysis. Two models, a stand photosynthesis model and a generic dynamic vegetation model (ORCHIDEE), were also applied in the analysis. EC data revealed that increasing autumn temperature significantly enhances TER: the temperature sensitivity was 9.5 gC m⁻² °C⁻¹ for the period September–October (early autumn when high radiation levels still occur) and 3.8 gC m⁻² °C⁻¹ for November–December (late autumn with suppressed radiation level). The cumulative GPP was practically independent of the temperature in early autumn. In late autumn, air temperature could explain part of the variation in GPP but the temperature sensitivity was very weak, less than 1 gC m⁻² °C⁻¹. The stand photosynthesis model predicted that under a prescribed 3–6 °C temperature increase, the temperature sensitivity of 4–5 gC m⁻² °C⁻¹ in GPP may appear in early autumn. The TER and GPP sensitivities, produced by the ORCHIDEE model, were similar to observed ones when the site level 1/2 h time step was applied, but the results calculated by using daily meteorological forcing, interpolated to 1/2 h time step, were biased stemming from the nonlinear relationship between the processes and the environmental factors.

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1 Introduction

The carbon balance of boreal forest ecosystems is sensitive to prevailing weather conditions. In the summertime these ecosystems are clear sinks of carbon, but in the winter they become small carbon sources because carbon uptake via photosynthesis decreases more than respiration (e.g. Suni et al., 2003; Lagergren et al., 2008). The timing of the sink-to-source and source-to-sink turning points in the autumn and spring depends on temperature (e.g. Pelkonen and Hari, 1980; Suni et al., 2003). Therefore, the annual balance is affected especially by the temperature in the autumns and springs (Mäkelä et al., 2006). During those periods, the difference in temperature sensitivity of photosynthesis and respiration processes is an important controller of the carbon balance.

According to future climate projections, boreal and arctic regions will be exposed to stronger warming than any other region of the world. The first signs of the high latitude warming are already observable (IPCC, 2007). According to the climate simulations, the mean annual air temperatures in Northern Europe are expected to increase between 2–6°C during this century and the increase is likely to be strongest during winter months (Christensen et al., 2007), lengthening the autumn period and making the spring start earlier. Over the past decade the autumn temperature has increased by almost 1°C over the Northern latitudes.

Recently, Piao et al. (2008) published results which showed that CO₂ records from the past 20 years exhibit a trend towards earlier autumnal carbon dioxide build-up in the atmosphere, a signal interpreted as resulting from increasing carbon losses from boreal forests ecosystems during warmer autumns. Overall, the earlier autumn build-up dominates over the earlier spring draw-down of CO₂, which means that the length of the net Carbon Uptake Period (CUP) has been shrinking over the past 2 decades. The CUP is defined as the duration of the period of the year during which the ecosystem is a net sink of atmospheric CO₂. According to Piao et al. (2008) the large scale inferences based on atmospheric CO₂ concentration records were partly corroborated by

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eddy covariance (EC) flux tower data from 24 northern ecosystem sites. The flux tower data from North American, Siberian, and Northern European boreal forests, all lumped together, suggested as well that the CUP terminates systematically earlier when autumn conditions get warmer. The strong positive temperature anomalies were associated with strong release of CO₂ to the atmosphere in autumn. However, the strongest negative temperature anomalies, autumns with temperature more than 2°C below the average, did not provoke much larger CO₂ sink than normal, suggesting an asymmetric response of ecosystems to autumn temperature.

EC data represents net carbon exchange at ecosystem scale (net ecosystem exchange, NEE). Photosynthesis measured by that method corresponds to gross primary production (GPP) and total ecosystem respiration (TER) is the sum of two respiration processes, autotrophic and heterotrophic one. GPP depends strongly on the intensity of the solar radiation and the physiological state of the ecosystem, and water and nutrient availability (Hari and Kulmala, 2008). TER consists of respiration of both the aboveground biomass and the roots and the rhizosphere as well as decomposition in the soil. The respiratory processes are often considered as temperature-driven although they ultimately rely on substrate availability and are coupled with photosynthesis (e.g. Högberg et al., 2001).

Since the EC measurements of NEE cannot discriminate GPP and TER, the gross fluxes are usually estimated indirectly by means of night-time measurements or by model-assisted procedures (Reichstein et al., 2005). In the study by Piao et al. (2008), the ORCHIDEE terrestrial ecosystem model was utilized in quantification of processes through which autumn warming controls GPP and TER separately. The model results suggested that the reason for elevated carbon losses in warm autumns is the stronger positive temperature sensitivity of TER compared to GPP. In the autumn, the day length has been used as a proxy for GPP limitation (Suni et al., 2003; Mäkelä et al., 2006; Bergeron et al., 2007). Thus, any changes in temperature are likely to be more strongly reflected in respiration rate rather than in assimilation.

The model analysis performed by Piao et al. (2008) was focused on a biome-scale

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response of boreal and temperate forests but did not look into any specific features of an individual ecosystem. Acquiring greater understanding of responses of an individual ecosystem to autumn warming is important for defining more realistic scenarios of ecosystem-specific climate-change induced alterations and for future developments of generic simulation models. The aim of this paper is to answer to these needs as regard to a Scots pine forest, which is one of the main ecosystem types at the boreal region. The boreal coniferous forests are widely distributed vegetation type in the world covering approximately 10 million km², 7% of the earth land surface (FAO, 2000). Boreal forest soils are among the largest terrestrial carbon pools, estimated to contain approximately 15% of the soil C storage world wide (Schlesinger, 1977; Post et al., 1982). In this study we analyze the effect of autumn climate, temperature in particular, to the carbon balance of a boreal Scots pine forest located in Hyytiälä, Southern Finland. We quantify the sensitivity of the ecosystem respiration, gross-primary productivity and the net carbon balance (NEE) to their environmental drivers utilizing eleven years of EC data. In order to separately analyze the factors behind the year-to-year variation in autumn GPP we applied two models, the stand photosynthesis model (Vesala et al., 2000, Kolari et al., 2006) and the dynamic global vegetation model ORCHIDEE (Krin-ner et al., 2005), for estimating stand GPP. The stand photosynthesis model is applied for the temperature sensitivity using simple temperature scenarios. The performance of the ORCHIDEE model, for predicting responses of the studied pine forest, is tested against the obtained results.

2 Materials and methods

2.1 Site description

The SMEAR II station is located in a relatively homogenous Scots pine stand (*Pinus sylvestris* L.) sown in 1962 next to the Hyytiälä forest station of the University of Helsinki in southern Finland (61°51' N, 24°17' E, 181 m a.s.l.). From 1970 to 2000, the site mean

annual temperature was +3.3°C and precipitation 713 mm. The mean depth of the soil organic layer is 5.4 cm and density 0.13 g cm⁻³. The forest floor vegetation is dominated by dwarf shrubs and mosses (Kulmala et al., 2008). According to the Cajander site classification system based on ground vegetation species composition (Cajander, 1909), the stand is of medium quality and has a current growth rate of 8 m³ ha⁻¹ yr⁻¹. The forest is in the middle of its commercial rotation time for this type of stand. It has been regenerated according to standard silvi-cultural guidelines (Peltola, 2001) and is therefore representative for a typical managed pine forest. The mean tree height has increased from about 13 to 16 m during the eleven-year period studied since 1996. The total leaf area index (LAI) varied from 6 to 8 m² m⁻²; in winter 2002, some parts of the stand was thinned and ~26.5% of the tree biomass was removed. The thinning had no detectable effect on NEE compared to the natural inter-annual variability (Vesala et al., 2005), but it resulted in a momentary decrease in LAI. However, the earlier level in LAI was re-established in a few years.

2.2 Data processing and modelling

2.2.1 Eddy covariance data and its partitioning and gap filling

The basic dataset used in this study consists of eleven years of 1/2-hourly CO₂ flux measurements of the net ecosystem exchange (NEE) complemented by climate and ecosystem data. In this study we utilize the eddy covariance (EC) data from 1997 to 2007. The flux measurements were made above the forest at 23.3 m height (at 46.6 m – from October 1998 through June 2000). The measurements, data processing and flux calculations are performed according to standard procedures (Aubinet et al., 2000) and the details of the measurement setup are described, for instance, in Markkanen et al. (2001). The half-hourly averaged fluxes were filtered for low turbulence conditions (u_* -threshold) as described in Markkanen et al. (2001) and corrected for changes in storage of CO₂ below the measuring height. The autumn is defined here as 1 September to 31 December and in some of the analyses the two-month periods

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September–October and November–December are considered separately.

Partitioning of NEE into TER (R_e) and GPP (P) was done as in Kolari et al. (2009). R_e was modelled using a modified Arrhenius type exponential equation (Lloyd and Taylor, 1994):

$$R_e = R_{e,0} e^{E(1 - \frac{T_0}{T_s})} \quad (1)$$

where T_s is temperature ($^{\circ}\text{C}$) at a depth of 2 cm in the soil organic layer, $R_{e,0}$ the average night-time turbulent flux at soil temperature T_0 , and E a temperature sensitivity parameter.

Half-hourly fluxes fulfilling the turbulence criteria were used for deriving GPP (P) directly from the measured NEE (F) as

$$P = -F + R_e \quad (2)$$

During periods of weak turbulence, GPP was replaced by modeled stand photosynthesis as a saturating function of light with a nonrectangular hyperbola

$$P = \frac{1}{2\theta_{\text{con}}} \left[\alpha I + P_{\text{max}} - \sqrt{(\alpha I + P_{\text{max}})^2 - 4\theta_{\text{con}}\alpha I P_{\text{max}}} \right], \quad (3)$$

where I is the incident photosynthetically active radiation (PAR, $\mu\text{mol m}^{-2} \text{s}^{-1}$), P_{max} ($\mu\text{mol m}^{-2} \text{s}^{-1}$) the rate of saturated photosynthesis, θ_{con} (dimensionless) a parameter defining the convexity of the light response curve, and α (dimensionless) the initial slope of the curve. The model parameters were derived from GPP estimates from measured fluxes and measured light values.

The temperature sensitivity of ecosystem respiration was derived from regressions of accepted night-time turbulent fluxes and temperature in the soil organic layer over the growing season. To take into account the inter-annual and seasonal variations in the photosynthetic light response and respiration, the base level of respiration $R_{e,0}$ and the parameters α and P_{max} in the photosynthesis model were estimated for each day of the year using a 9-day moving window of accepted flux data. The parameters were

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estimated simultaneously using both night-time and daytime measurements within the same time window (more detailed description in Kolari et al., 2009).

2.2.2 Stand photosynthesis model

We estimated stand GPP using a model for photosynthesis of the tree canopy and the forest floor vegetation (Vesala et al., 2000; Kolari et al., 2006). The photosynthesis component of the model combines the optimal stomatal control model (Hari et al., 1986) with an annual cycle model (Mäkelä et al., 2004). The key parameter that varies seasonally in the optimal stomatal control model is photosynthetic efficiency β that varies seasonally. Mäkelä et al. (2004) found that the autumnal variation in photosynthetic efficiency in boreal Scots pine can be accurately explained by ambient temperature history S by

$$\frac{dS}{dt} = \frac{T - S}{\tau} \quad (4)$$

where T ($^{\circ}\text{C}$) is the ambient air temperature and τ a time constant (200 h). In the model simulations, S for each moment of time i was calculated with a time step Δt of 30 min

$$S_i = S_{i-1} + \frac{T_i - S_{i-1}}{\tau} \Delta t \quad (5)$$

The initial value of S was set equal to the first temperature record of the climatic data. The relationship between S and daily photosynthetic efficiency β was modeled as a sigmoidal response to temperature history (Kolari et al., 2007).

$$\beta = \frac{\beta_{\max}}{1 + e^{b(S-T_s)}} \quad (6)$$

where β_{\max} is the seasonal maximum of photosynthetic efficiency. T_s ($^{\circ}\text{C}$) is the inflection point, i.e. the value of S at which β reaches half of β_{\max} , and b curvature of the function. The slow temperature response was further modified by introducing the

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instantaneous response of β to freezing temperatures and the carry-over effect from nighttime frost (Kolari et al., 2007), as a multiplier that varied between 0 and 1. The value of the frost modifier was 1 if the minimum air temperature in the previous night was above zero. Below 0°C the modifier decreased linearly with temperature, reaching zero at -10°C. The values of the photosynthetic model parameters and the annual cycle parameters were based on gas exchange measurements with chambers on several pine shoots in Hyytiälä in 2000–2005 (Kolari et al., 2007).

The stand photosynthesis model was applied in half-hour time steps over the autumns (September–December) of 1997–2007. The model input included meteorological data measured at the site with all half-hourly temperature records raised by the increase in annual mean temperature for different climate warming scenarios (present, 3°C and 6°C). The relative humidity remained unaltered and the present-day atmospheric CO₂ data was used to extract the effect of temperature on photosynthesis.

2.2.3 Global vegetation model

The ORCHIDEE model (Krinner et al., 2005) represents key vegetation processes governing terrestrial biogeochemistry and biogeography. ORCHIDEE consists of five vegetation carbon reservoirs, four litter reservoirs, and three soil reservoirs. Plant CO₂ assimilation in ORCHIDEE model is based on work by Farquhar et al. (1980) for C3 plants and Collatz et al. (1992) for C4 plants. Maintenance respiration is a function of each living biomass pool and temperature, while growth respiration is computed as a fraction of the difference between assimilation inputs and maintenance respiration outputs to plant biomass. Heterotrophic respiration parameterization is taken from CENTURY (Parton et al., 1988). Here, we performed two simulations at different time steps: half hourly and daily time step. In each simulation, we first run the model until ecosystem carbon pools reach steady-state equilibrium (long-term mean annual NEE≈0), using the observed corresponding meteorology data (half hourly or daily data) for 1997. Starting from this equilibrium state, the model is integrated for ten years 1997–2006 forced by observed historical climate data.

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3 Results

3.1 Climate conditions

There were three distinguishable years in terms of climate extremes in the autumn (Fig. 1). Autumn 2002 was exceptionally dry and cool whereas autumns 2000 (not shown separately) and 2006 were warm and moist. The autumn 2006 was significantly warmer than average especially in December whereas 2002 was colder than average in October–December. The large positive anomaly in December 2006 is apparent also in soil temperature (T_s) (Fig. 1b). In general, air temperature (T_a) decreased gradually during the autumn from ~ 12 – 20°C in early September to -15 to $+1^\circ\text{C}$ in late December. Similarly to T_a , T_s decreased from values around 11 – 14°C to 0 to $+2^\circ\text{C}$ during the course of the autumn. Soil temperature seldom reached the freezing point because of the insulating effect of snow and large heat capacity of the moist soil. Only in 2002 soil frost occurred because of low soil moisture content (θ) (see Sevanto et al., 2006). The global radiation (R_g) decreased rapidly from September to November because of the northern location of the site (Fig. 1c). The inter-annual variability in R_g is relatively large in early autumn with the extremes occurring in 2001 and 2003 (cloudy) and 1999 and 2000 (clear) (the values not shown). The θ varies strongly both within and between the autumns (Fig. 1d). Typically θ is lowest ($\sim 0.2 \text{ m}^3 \text{ m}^{-3}$) at the end of the summer and a gradual recharge of the water content occurs in late September–November depending on the amount of precipitation. The extreme years in terms of soil moisture content were 1998 (moist) and 2002 (dry and cold). In summer 2006 the forest was suffering from intensive drought (not shown), which reduced both the ecosystem respiration and gross photosynthesis and turned the stand to be a carbon source (Duursma et al., 2007) over two weeks in August. As a consequence, the early autumn (September–October) 2006 has the lowest θ values but in November the soil moisture content returned to the typical level.

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3.2 Temporal variability of GPP and TER

Similarly to the climatic variables we show the general behavior and the extreme values of carbon cycle components during 1 September–31 December in 1997–2007. The mean 14-day NEE (Fig. 2a) varied from -0.3 to $-2.2 \mu\text{mol m}^{-2} \text{s}^{-1}$ (average $-1.2 \mu\text{mol m}^{-2} \text{s}^{-1}$) in early September and remained negative in most of the years until early October when the ecosystem turned into a cumulative source for atmospheric CO_2 (Fig. 2b). In late autumn (November–December) the temporal variability of NEE was small. However, the exceptionally warm December 2006 differed from the other years by high respiration values, whereas the cold December 2002 was accompanied by somewhat lower NEE values than the average. The CUP end was defined as the last day when 5-day average NEE was negative (Piao et al., 2008). On average, it occurred on day 284 (11 October). The earliest CUP end was on day 272 (29 September) in 1999 and 2006 and latest on day 295 (22 October 2005). However, there was no correlation between CUP end and mean autumn temperature, which was defined in 60-day window around the mean CUP ending.

The mean 14-day (nights included) GPP varied from 6.5 to $4.7 \mu\text{mol m}^{-2} \text{s}^{-1}$ in early September to less than $0.2 \mu\text{mol m}^{-2} \text{s}^{-1}$ in December (Fig. 2c). The inter-annual variability in GPP in early autumn was strongly linked to changes in radiation (Fig. 1c). The years with lowest R_g had generally the lowest GPP (2004, 2003 and 2001) (not shown). In particular, the strong decrease in photosynthesis in mid-September 2001 (lowest Sept value in Fig. 2c) was caused by an extremely cloudy period. The major fraction of the autumnal carbon assimilation happened in early autumn (September–October). Also the inter-annual variability was much larger in absolute terms in September–October period than in November–December. Late autumn (November–December) contributed only between 1% (2002) to 7% (2004) to the total autumn GPP (Fig. 2d). Therefore, the climate changes taking place in late autumn seems likely to have negligible effect on annual budget of GPP, which is confirmed by the model analysis later.

TER followed closely the course of the soil (and to some extent air) temperature with

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highest 14-day average values ($3.7\text{--}5.1 \mu\text{mol m}^{-2} \text{s}^{-1}$) in early September (Fig. 2e). The inter-annual variability of TER, both in absolute and relative terms was markedly larger than in GPP, especially in late autumn. The carbon emissions during cool and dry 2002 were consistently smaller than in other years (Fig. 2f). In proportion, the moist and warm autumns 2000 (not shown) and 2006 had the highest cumulative respiration. Contrary to GPP, the late autumn contributed significantly to the autumnal ecosystem respiration – the contribution varied from 20% (2002) to 29% (2003).

3.3 Temporal correlation of GPP and TER with temperature and radiation

GPP correlated best with T_a in the spring, but in the autumn it was mostly determined by radiation (Fig. 3). The r was calculated from daily averages in a 30-day moving window; e.g. the plotted value for 30 September is the linear correlation coefficient of daily averages in the window 1–30 September, concatenated over the years 1996–2007. Here year 2006 was omitted because a separate analysis revealed that the strong drought anomaly in the late summer (August) of 2006 affected significantly the results. The correlation between GPP and the air temperature was in the order of +0.5 to 0.7 in the spring (March–May). As the growing season progressed, the correlation between GPP and T_a decreased and the correlation with PAR increased peaking in September–October ($>+0.8$). Thus, the primary driving factors in springtime and later in the summer were different. During the rest of the year (winter and late autumn) both correlations remained small, less than 0.4, but GPP itself was also very small (Fig. 2c). The correlation between TER and the soil temperature was strongest ($r \sim +0.9$) in May and early autumn (September–November) but dropped slightly in July–August because that period is often dry and soil moisture limitations restrict TER. In December the correlation between TER and T_s decreased rapidly and remained small through the winter, while the respiration level was low and the soil temperature stable. Note that the environmental factors are also correlated. Most importantly, the relationship between daily radiation and temperature depends on the season. In summer the clear skies

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(high radiation) lead to larger daily average temperatures ($r \sim +0.5$) while during the winter and autumn the clear days are typically cold ($r \sim -0.5$) and the warm spells are associated with westerlies from the North Atlantic, which typically create cloudy and moist conditions at the region.

To summarize the Fig. 3, Table 1 shows the average correlation coefficients between cumulative carbon balance components and mean climate parameters in early (September–October) and late autumn (November–December) periods. The r between TER and soil and air temperature was high (around + 0.8, $p < 0.01$) both in the early and late autumn. The correlation between GPP and temperature was low in early autumn but became statistically significant in November–December ($p < 0.05$). The correlation between GPP and PAR (+0.56) was not significant ($p > 0.05$) in early autumn but when the influence of temperature was removed (partial correlation), it became significant (+0.64, $p < 0.05$). The r between GPP and temperature was significant ($\sim +0.7$, $p < 0.05$) in late autumn and the correlation with PAR was negligible. The mean temperature and radiation (PAR) were negatively, although not statistically significantly ($p > 0.05$), correlated (~ -0.5) both early and late in the autumn which is important considering the different roles of temperature and PAR regulating the carbon exchange.

3.4 Temperature sensitivity of measured GPP and TER

A distinct relationship between average T_a and the cumulative NEE existed for both early and late autumn periods (Fig. 4a). The correlation was higher for November–December when GPP was very small and NEE was practically the same as respiration, which depends on temperature. The temperature sensitivity of the early autumn was more than $8 \text{ gC m}^{-2} \text{ }^\circ\text{C}^{-1}$ whereas it was close to $3 \text{ gC m}^{-2} \text{ }^\circ\text{C}^{-1}$ in the late autumn. The cumulative GPP was practically independent of the temperature in the early autumn ($R^2 = 0.02$) (Fig. 4b). In the late autumn the air temperature could explain 43% of the variation in GPP ($R^2 = 0.43$) but the temperature sensitivity was very weak, less than $1 \text{ gC m}^{-2} \text{ }^\circ\text{C}^{-1}$. The highest R^2 values existed for R_e and the temperature

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sensitivity was almost $10 \text{ g C m}^{-2} \text{ }^\circ\text{C}^{-1}$ for September–October ($R^2=0.69$) and almost $4 \text{ g C m}^{-2} \text{ }^\circ\text{C}^{-1}$ for November–December ($R^2=0.65$) (Fig. 4c).

3.5 Modelled temperature dependence of GPP in future scenarios

The results above show that both the GPP and its temperature sensitivity were very small in the late autumn during the past eleven years. The small apparent temperature sensitivity can be largely attributed to the negative correlation of radiation and temperature in autumn (see Fig. 3 and Table 1). It is plausible that during colder periods, there are more night frosts that drop the day-time light use efficiency. However it cannot be used as such to predict the response of GPP to the climatic warming. Therefore, we consider next the GPP-temperature relationships in the present (past 11 years) climate and then under the elevated temperatures using the stand photosynthesis model. The purpose here is to obtain the order of magnitude estimates for temperature sensitivity and thus the scenarios are simplified and include only the constant increase of the temperature by 3 or 6° from the present 1/2 h temperature records. Nevertheless, the used procedure is realistic enough to reveal interplay of GPP and temperature if the radiation and relative humidity would not change. The modeling results for the past 11 years were consistent with the measured fluxes (see Figs. 4 and 5). Daily GPP diminished steeply in autumn with lower PAR and shorter daylight hours. Even on clear days with temperature clearly above zero, GPP in November and December was very low. The temperature sensitivity of the modeled GPP was of the same order of magnitude as the measured in present climate. There was no clear correlation between the mean temperature and GPP in early autumn (September–October, $R^2=0.23$) although the slope ($+4.7 \text{ g C m}^{-2} \text{ }^\circ\text{C}^{-1}$) is steeper than measured $+1.1 \text{ g C m}^{-2} \text{ }^\circ\text{C}^{-1}$ (Fig. 3b). In the late autumn (November–December) the GPP-T relationship was more distinct but the absolute GPP so small that the increase in GPP per unit temperature was less than $0.6 \text{ g C m}^{-2} \text{ }^\circ\text{C}^{-1}$. In the model, the cold autumn of 2002 had not the lowest GPP because the early autumn was sunny. When all half-hourly temperatures were increased

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by 3°C and 6°C, the modeled GPP increased by about 4.5 g C m⁻² °C⁻¹ ($R^2=0.23$) in September–October and 1.1 g C m⁻² °C⁻¹ in November–December ($R^2=0.68$). We assumed that the diurnal and the seasonal patterns of radiation remain the same in the warming climate. It is possible; however, that with increasing temperature the cloudiness also increases which will reduce the predicted increase in GPP.

3.6 Sensitivity tests by the dynamic global vegetation model

The model runs by the dynamic global vegetation model (ORCHIDEE) were carried out using both daily and 1/2 hourly meteorological forcing. The modeled response of NEE to temperature change varied with the simulation time step (Fig. 6). For example, early autumn NEE derived from the simulation using 1/2 hour forcing was increased in response to rising temperature by 5 g C m⁻² °C⁻¹ ($R^2=0.11$), while simulation using daily forcing gave early autumn NEE to be negatively related to temperature (-2 g C m⁻² °C⁻¹, $R^2=0.09$). Such different response of NEE to early autumn temperature change was mainly due to the different response of GPP. In response to rising temperature, daily time step showed higher sensitivity of GPP (13 g C m⁻² °C⁻¹, $R^2=0.96$) than half hourly time step simulation (3 g C m⁻² °C⁻¹, $R^2=0.09$). For TER the modelled sensitivity was similar between half hourly time step simulation (8 g C m⁻² °C⁻¹) and daily time step simulation (11 g C m⁻² °C⁻¹). The 1/2 hourly forcing produced results which were closer to the observed relationships (see Fig. 5).

4 Discussion

It was revealed that the correlation between GPP and TER with the driving environmental factors changes intra-annually as well as during the autumn period September–December, when the air temperature and insolation drastically decreases. The outcome of the complicated non-linear dynamics is that the autumnal cumulative NEE and TER are significantly larger if the average air temperature is higher, while the effect of

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the temperature to the cumulative GPP is much weaker. This leads to the situation that during warmer autumns the studied pine forest (soil) is releasing larger amounts of carbon to the atmosphere.

In early autumn the correlation between GPP and the air temperature was generally smaller than 0.2 while the correlation with radiation was around +0.8. In October the correlation coefficient with the radiation decreased rapidly below the 0.5 level and gradually to zero during the late autumn. At the same time when the correlation with radiation dropped, the correlation of GPP with temperature increased rapidly and peaked to 0.5 in the middle of November. Also, the relationship between daily mean temperature and radiation changed during the autumn. In early September, high air temperature was associated with clear skies and the correlation between GPP and air temperature was slightly positive ($r \sim +0.3$) whereas in late autumn the correlation was negative (-0.6 in December). This behavior was caused by the appearance of the synoptic scale lows associated with warm westerlies coming from the North Atlantic that bring moist and warm air and produce cloudy skies over the Scandinavia. Thus, the warmest periods in late autumn and wintertime were typically associated with high cloudiness and large precipitation, conditions favorable for relatively high decomposition rates, of which contribution to TER is large in the autumn.

The highest temperature sensitivity for TER, almost $10 \text{ gC m}^{-2} \text{ } ^\circ\text{C}^{-1}$, was found for September–October period. In late autumn the temperature sensitivity about $4 \text{ gC m}^{-2} \text{ } ^\circ\text{C}^{-1}$ was close to the regional sensitivity found in Piao et al. (2008). The measured sensitivity of GPP at the same periods was only the order of $1 \text{ gC m}^{-2} \text{ } ^\circ\text{C}^{-1}$. From the apparent temperature responses one could conclude that TER will increase more than GPP, implying that net ecosystem productivity will be reduced if autumn temperatures rise. However, plant respiration can also acclimate to changing temperature regimes (Atkin and Tjoelker, 2003). Furthermore, respiration and NEE are determined not only by environmental driving factors but also by the availability of photosynthates and demand for energy in the plant tissues (Gifford, 2003). The proportion of autotrophic respiration to GPP should be fairly stable when integrated over long pe-

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riods of time, respiration being constrained by GPP (e.g. Dewar et al., 1998). Waring et al. (1998) suggested that net primary productivity, and correspondingly respiration, would be a constant ratio of GPP. Recently, a synthesis study over wide range of vegetation types showed a tight (positive) correlation between annual GPP and TER; a year-to-year differences in assimilation explained ~60% of the inter-annual variability in respiration (Baldocchi, 2008). As a large part of CO₂ efflux from heterotrophic respiration originates in prompt utilization of recently produced photosynthates (root exudates) (Pumpanen et al., 2008, 2009) also long term TER would be roughly proportional to GPP. This means that in a warming climate the temporal distribution of the decomposition may change within a year although not necessarily the total cumulative decomposition. The stock of easily decomposable carbon would be exhausted already in the autumn and the soil CO₂ efflux in spring would be correspondingly lower. In dark but warm winters the proportionality of annual respiration and GPP might break, however. Another issue is the delayed effects. Autumn 2002 was the coldest year during the both periods and 2006 the warmest one for September–October and the second warmest for November–December, only 2000 was a bit warmer for the later period. Despite same temperature and moisture conditions, TER in December 2006 was much larger than in 2000. This may be because there could have been excess of rapidly decomposing litter left in the ground in autumn 2006 in the wake of the intensive August drought that strongly decreased both respiration and assimilation. Thus, the history of the ecosystem cannot be ignored.

The photosynthesis model combined with the simple climate scenarios of 3 and 6° temperature increases predicted that while measured autumnal GPP was rather insensitive to the temperature under the present temperature regime, GPP did seem to have the temperature dependence even for November–December period when larger temperature range is considered. Note that the effects of atmospheric CO₂ fertilization on photosynthesis and respiration are not considered here, neither the any carbon-nitrogen coupling (see e.g. Hari and Kulmala, 2008). The temperature sensitivities of the cumulative GPP and TER calculated by the dynamic global vegetation model were

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similar to the observation, when the $1/2$ h time-step was used. However, the results using daily forcing data were biased towards too high temperature dependence of GPP leading to too low temperature dependence of NEE. The bias stems from the non-linear relationships between the processes and the environmental factors. This result not only implies that current biogeochemical models working on daily time steps (e.g., LPJ by Sitch et al., 2003; CASA by Potter et al., 1993; TEM by Mellilo et al., 1993) may be not able to correctly capture the response of carbon cycle to climate change, but also highlights the importance of accurate forcing data in current model application for projection of future carbon cycle. Monthly time step of climate data is generally used in IPCC future scenarios of carbon cycle.

5 Conclusions

The flux observations show that increasing autumn temperature enhances carbon efflux from the studied ecosystem, because respiration (TER) is strongly temperature dependent and it dominates over photosynthesis (GPP) especially during late autumn when radiation levels are low. However, it is not clear whether warm autumns increase overall carbon losses from the forest, or whether autumnal losses are counterbalanced by lowered respiration levels in the following spring. According to our stand photosynthesis model, a prescribed increase of $3\text{--}6^\circ\text{C}$ in the air temperature would lead to more pronounced temperature sensitivity GPP, although still weaker than that of TER, in early autumn. This is partly due to diminishing of the frosting temperatures suppressing GPP: the generic dynamic vegetation model ORCHIDEE produced similar TER and GPP temperature sensitivities, to observations, when the $1/2$ h time-step was applied, but the daily time step strongly overestimated the GPP temperature dependence.

Acknowledgements. This research was supported by the Academy of Finland Center of Excellence program (project numbers 1118615 and 7523004), by the Academy of Finland project 213093 and by the Nessling Foundation (project 2009067 “Improving the biosphere description of global climate models”). EU projects IMECC and ICOS are also acknowledged.

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Table 1. Bivariate correlation coefficients ($N=11$) between cumulative carbon balance (NEE), its components (GPP, TER) and mean climate variables air (T_a) and soil temperature (T_s), photosynthetically active radiation (PAR) and volumetric soil moisture content (θ) in early (September–October) and late autumn (November–December). Statistically significant correlations are marked with ** (2-tailed $p<0.01$) and * ($p<0.05$).

	NEE	GPP	TER	T_a	T_s	PAR	θ
Early autumn							
NEE	1	-0.40	0.79(**)	0.69(*)	0.77(**)	-0.79(**)	0.35
GPP	-0.40	1	0.25	0.14	0.09	0.53	-0.23
R_e	0.79(**)	0.25	1	0.83(**)	0.88(**)	-0.46	0.18
T_a	0.69(*)	0.14	0.83(**)	1	0.94(**)	-0.39	0.27
T_s	0.77(**)	0.09	0.88(**)	0.94(**)	1	-0.56	0.23
PAR	-0.79(**)	0.53	-0.46	-0.39	-0.56	1	-0.52
θ	0.35	-0.24	0.18	0.27	0.23	-0.52	1
Late autumn							
NEE	1	0.67(*)	0.99(**)	0.80(**)	0.78(**)	-0.21	0.32
GPP	0.67(*)	1	0.79(**)	0.66(*)	0.71(*)	-0.10	0.57
R_e	0.99(**)	0.79(**)	1	0.81(**)	0.81(**)	-0.19	0.38
T_a	0.80(**)	0.66(*)	0.81(**)	1	0.86(**)	-0.47	0.59
T_s	0.78(**)	0.71(*)	0.81(**)	0.86(**)	1	-0.54	0.60
PAR	-0.21	-0.10	-0.19	-0.47	-0.54	1	-0.25
θ	0.32	0.57	0.38	0.59	0.60	-0.25	1

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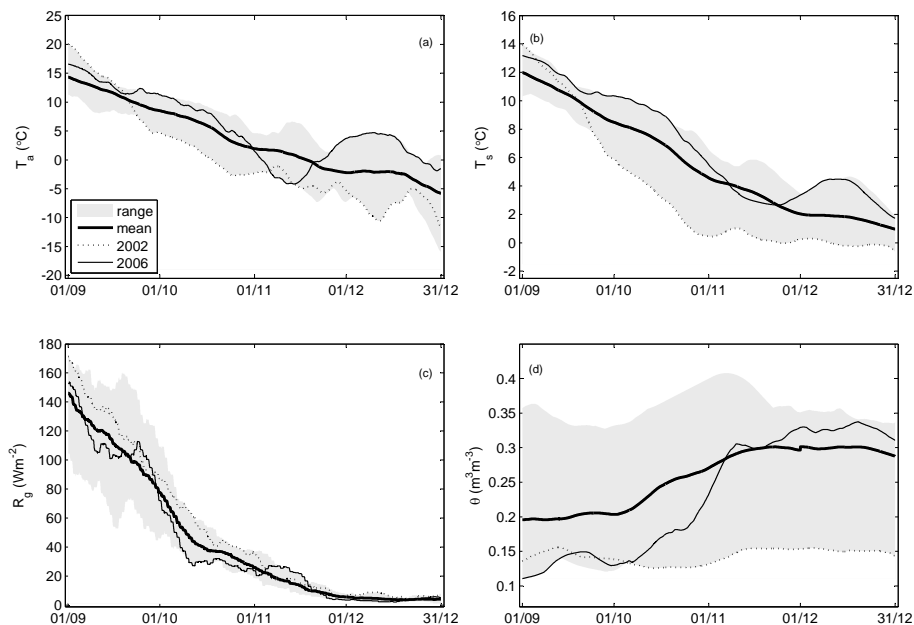


Fig. 1. The climate conditions. **(a)** air temperature (T_a), **(b)** soil temperature (T_s), **(c)** global radiation (R_g) and **(d)** volumetric soil water content (θ). The average and the extreme years (2002 and 2006) are shown separately and the shaded area shows the variability range during 1997–2007. All values are 14-day running averages.

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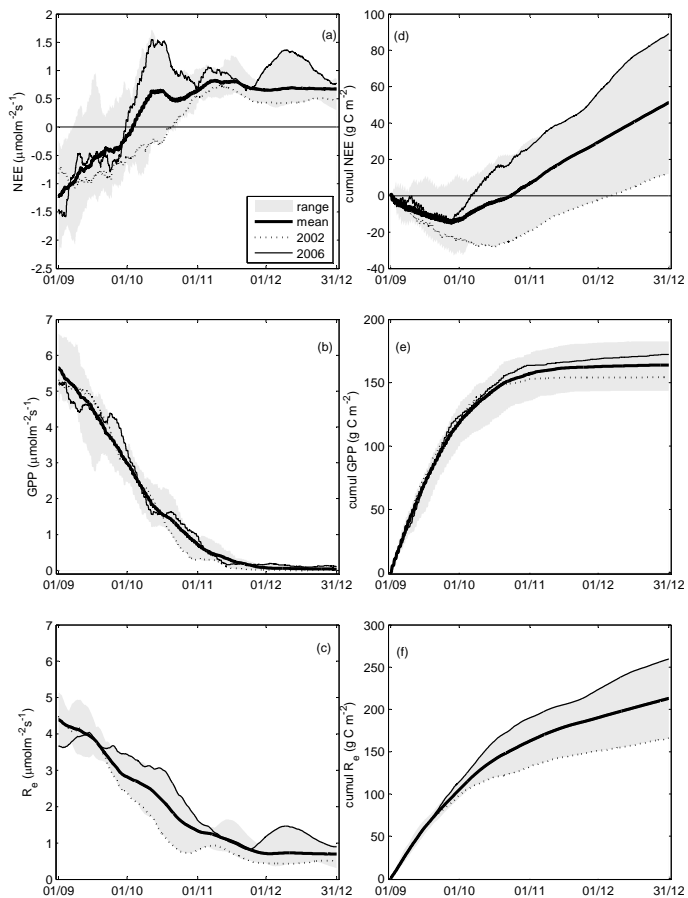


Fig. 2. Net ecosystem exchange (NEE), gross primary productivity (GPP) and ecosystem respiration (R_e) as 14-day running mean (left) and their cumulative values (right). The symbols are as in Fig. 1.

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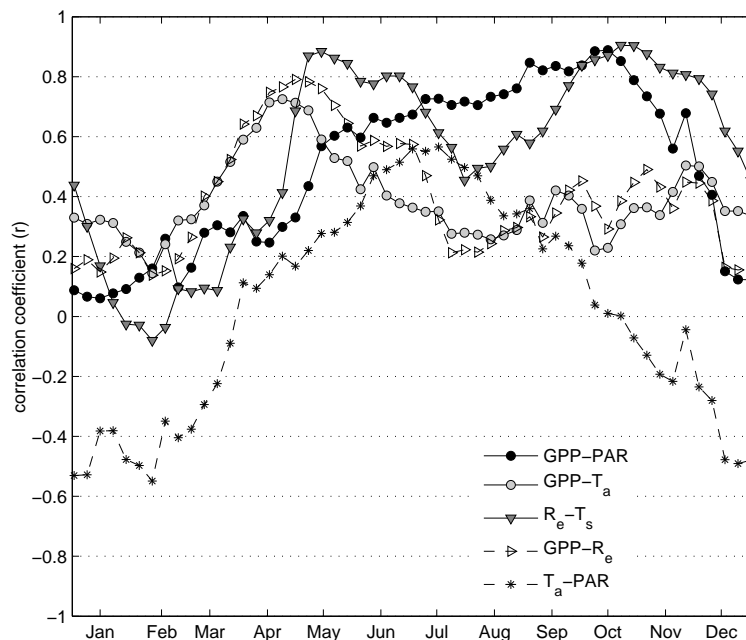


Fig. 3. Temporal variation of the correlation coefficient (r) between GPP and R_e and their expected drivers: air temperature (T_a), soil temperature (T_s , B-horizon, 10–25 cm depth) and photosynthetically active radiation (PAR). r is calculated from daily mean values within a 30-day moving window (29 day overlap) using data from years 1997–2005 and 2007. Values of r are shown at 7 day intervals.

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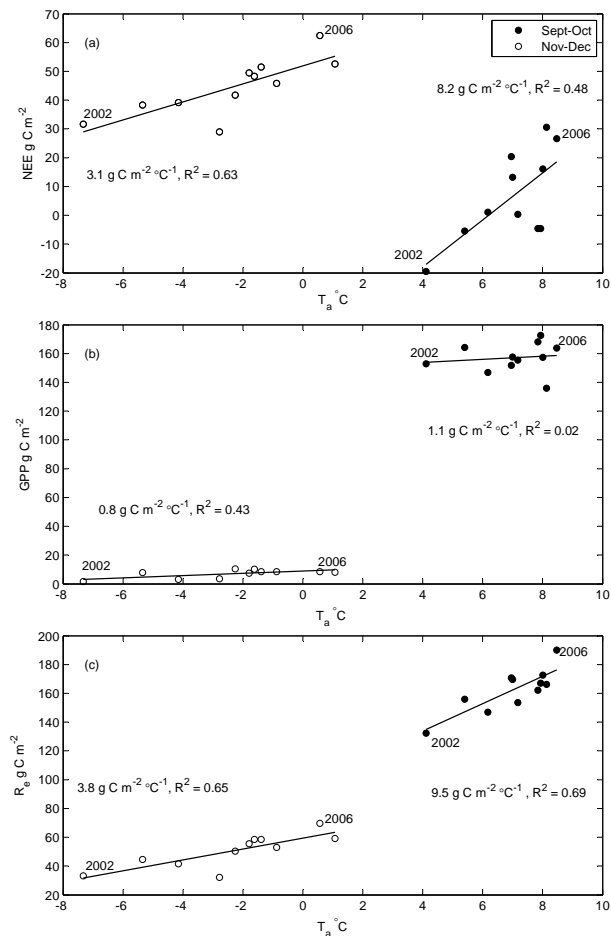


Fig. 4. Cumulative NEE (a), GPP (b) and R_g (c) over the early (September–October) and late autumn (November–December) as a function of the average air temperature (T_a) for the corresponding bimonthly periods. The linear least-squares regressions give the temperature sensitivities.

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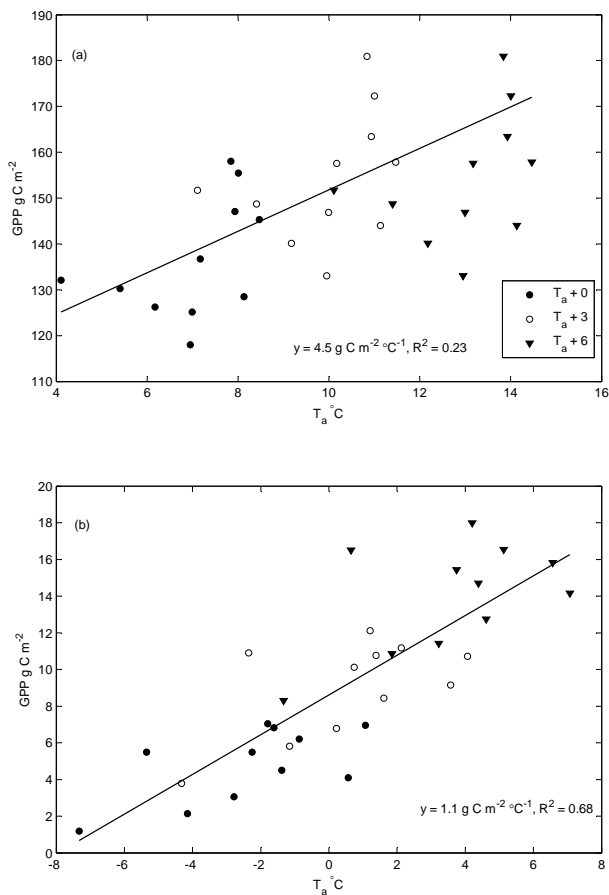


Fig. 5. Modeled cumulative GPP as a function of mean air temperature (T_a) in early (September–October) (a) and late autumn (November–December) (b) periods. The different symbols show the three temperature scenarios (present, +3°C and +6°C). The linear least-squares fit show the average temperature sensitivity over all data points in each panel.

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Warming and carbon balance of a boreal pine forest

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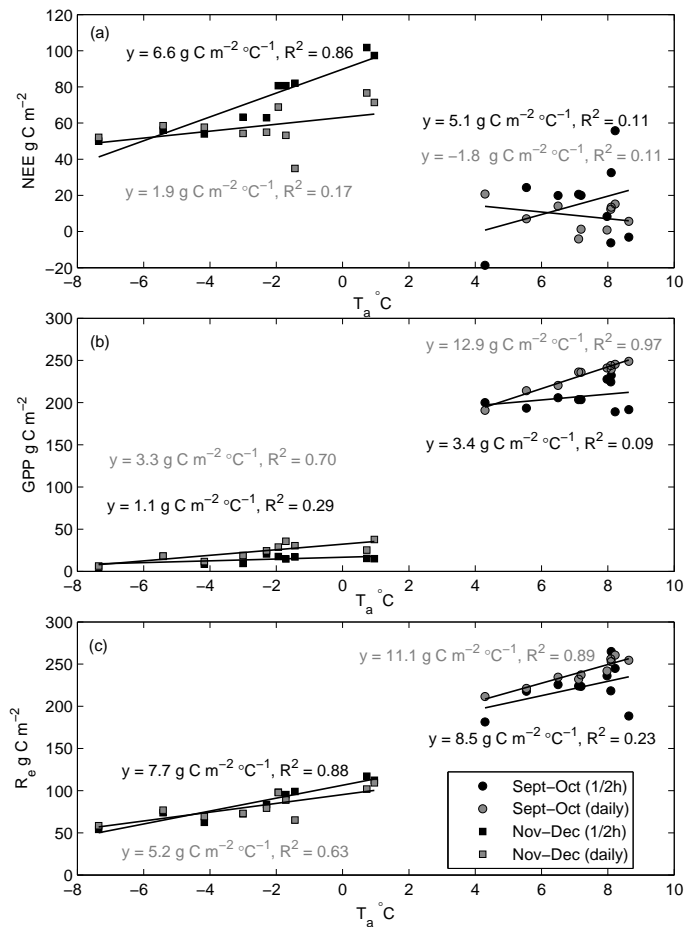


Fig. 6. Relationship of ORCHIDEE modeled NEE (a), GPP (b), and TER (c) with temperature in early (September–October) and late autumn (November–December) periods. Two simulations at different time steps with half hourly (black) and daily (grey) time step are performed.

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