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Discussions

Effects of climate variability and functional changes on the interannual variation of the carbon balance in a temperate deciduous forest

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Abstract

The net ecosystem exchange of CO_2 (NEE) between the atmosphere and a beech forest (Sorø, Denmark) showed significant interannual variation (IAV) over 13 years (1997–2009) of observations. The forest sequestered, on average, 157 g C m^{-2} yr^{-1}, ranging from a source of 32 to a sink of 344 g C m^{-2} yr^{-1} in 1998 and 2008, respectively. The objectives of this study were to evaluate to what extent and at which temporal scale, climatic variability (through direct response) and changes in ecosystem functional properties (through biotic response) regulated the IAV in the ecosystem carbon balance. To address this question, we performed correlation analysis between the carbon fluxes and climate variables at different time scales. The response of CO_2 exchange to climatic variability was significantly higher at short time scales and the limiting factors changed intra-annually. Combinations of climate anomalies in different periods of the year either intensified or attenuated the aggregated ecosystem responses, implying that the changing distribution of climate anomalies, in addition to the average climate change, could have stronger impacts on the ecosystem carbon balance in the future. A semi empirical model was used to estimate a set of parameter time series for each of the 13 years, which was considered to represent the functional properties of the ecosystem. The climate and parameter time series were applied factorially by year to quantify their relative importance for the IAV in carbon flux. At an annual time scale, as much as 77 % of the IAV in NEE could be attributed to the variation in both photosynthesis and respiration related model parameters, indicating a strong influence of functional change. The possible causes for the observed functional change could not be addressed with the available dataset. This demonstrates the need for more targeted experiments, such as long-term measurements of leaf nitrogen content. Our approach incorporated seasonal variation in the ecosystem status and demonstrated a significant role of biotic factors on the carbon dynamics in a typical temperate deciduous forest. The method can be applied at other sites to explore ecosystem behaviour across different plant functional types and climate gradients. Further, this approach

showed how important it is to incorporate functional change in process based models, which could guide model development and consequently reduce the uncertainties in long-term projection of global ecosystem carbon balance.

1 Introduction

Terrestrial ecosystems fix more than ten times the current annual anthropogenic carbon dioxide (CO_2) emission through photosynthesis (Beer et al., 2010; Friedlingstein et al., 2010). Meanwhile, a similar amount of CO_2 is released back to the atmosphere by respiration in soil and plants. The difference between these two opposing fluxes determines the net carbon balance of the ecosystem, which varies across time and space (Luyssaert et al., 2007; Stoy et al., 2009; Yuan et al., 2009). Small perturbations in the climate or ecosystem status may alter the equilibrium between photosynthesis and respiration. Whether the terrestrial ecosystems will act as a sink or a source of CO_2 is important because this net flux is of the same order of magnitude as the emission from fossil fuel combustion, which could either mitigate or amplify climate change. Therefore, understanding the spatiotemporal variability of the ecosystem carbon balance and the mechanisms that control it is crucial for assessing the vulnerability of the terrestrial carbon pools under future changing climate conditions (Reichstein et al., 2007; Heimann and Reichstein, 2008).

One important approach to understand the ecosystem carbon dynamics is to investigate the interannual variability (IAV) of net ecosystem exchange of CO_2 (NEE), with long-term eddy covariance measurements (Baldocchi, 2003). By analyzing the year to year variation in NEE under different climatic conditions, the key factors and processes that determine the ecosystem carbon balance can be identified. The measured NEE integrates gross primary production (GPP) and total ecosystem respiration (TER) which are both much larger than the net flux. The responses of GPP and TER to climate are complex. Some processes are direct and instantaneous, for instance the light response of photosynthesis and the kinetic sensitivity of photosynthesis (Sage and Kubien, 2007) and respiration (Mahecha et al., 2010) to temperature increase. However, there are also indirect responses, especially through changes in phenology (Richardson et al., 2010), canopy structure (Barr et al., 2004; Ibrom et al., 2006) or acclimation (Luo et al., 2001). Many studies have reported enhanced carbon uptake as warming extended the length of growing seasons (Chen et al., 1999; Black et al., 2000; Tanja et al., 2003; Hollinger et al., 2004; Churkina et al., 2005; Penuelas and Filella, 2009; Richardson et al., 2009; Pilegaard et al., 2011). Others show that distribution and intensity of precipitation can also indirectly affect ecosystem carbon balance because the induced water stress could alter the leaf area index (Le Dantec et al., 2000; Barr et al., 2007). These indirect responses are often not instantaneous but lagged. Hu et al. (2010) observed that reduced snow cover in the winter led to water stress in the following summer and hence limited photosynthesis in a subalpine forest. Also, climate anomalies (e.g. high temperature) in spring can increase photosynthesis in the following autumn, possibly due to enhanced leaf nitrogen content and canopy photosynthetic capacity as a result of increased nitrogen mineralization (Richardson et al., 2009).

To analyze the long-term climate change impacts on ecosystem carbon balance, it is important to jointly consider the direct, indirect and lagged responses to climate. However, to explicitly distinguish between these responses is difficult. Richardson et al. (2010) illustrated with four conceptual models that only phenological transitions (which is here defined as an indirect response) can have direct, indirect and lagged impacts on ecosystem productivities. In a simpler approach, Richardson et al. (2007) classified the ecosystem responses into direct and biotic responses to environmental forcing. The biotic responses were defined as parameters of the ecosystem models (e.g. maximum photosynthetic capacity and base respiration) which could be influenced by current and past climate conditions. IAV in biotic responses was regarded as functional change.

Partitioning the effects of direct climate variability and functional change on IAV in the carbon balance is important. It allows the evaluation of the necessity of incorporating

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functional change modules into mechanistic models, which are used to project future ecosystem carbon balance. Hui et al. (2003) used a homogeneity-of-slope model and a stepwise multiple regression approach to assess the IAV of the biotic responses of the ecosystem, concluding that functional changes account for about 10 % in the observed variation in the NEE at the Duke Forest. Richardson et al. (2007) concluded that it is important to consider the time scale when trying to partition the source of variance in NEE. With the parameters of a modified light response model fitted to NEE in each year, as much as 55 % of the variation could be attributed to the biotic responses at an annual time scale. In contrast, the effect of functional changes were found to be much lower in relatively undisturbed ecosystems such as peatland (Teklemariam et al., 2010).

Both the abiotic (i.e. direct) and biotic responses to climate variability have seasonal patterns. For instance, the limiting factor for photosynthesis may change at different periods of the year. Also, key parameters (e.g. maximum photosynthetic capacity) can vary seasonally (Hollinger et al., 2004; Wang et al., 2007; Thum et al., 2008). Therefore, the IAV of carbon balance should be analyzed not only at annual but also at sub-annual time scales (e.g. weekly, monthly or seasonally). Piao et al. (2008) suggested the warming effect in autumn accounts for the annual carbon loss (with a sensitivity of 0.2 Pg C °C^{-1}) in northern terrestrial ecosystems. This was supported by a site level study where the autumn temperature dominated the annual carbon balance (Vesala et al., 2010). To analyze the ecosystem response in different seasons is of interests.

At a temperate beech forest near Sorø, Zealand Denmark, NEE was continuously measured over the past 13 years (1997–2009). The annual NEE ranged from a source of 32 g C m^{-2} yr^{-1} in 1998 to a sink of −344 g C m^{-2} yr^{-1} in 2008 (negative sign as a sink). A decadal trend of NEE at this site has been reported by Pilegaard et al. (2011), with an average increase of −23 g C m^{-2} year^{-2}. While no significant change in the leaf area index was observed, the analysis indicated that an extended carbon uptake period and an increase in the maximum photosynthetic capacity during the growing season were responsible for the trend. The aim of this study was to investigate the IAV of carbon fluxes at Sorø with respect to (1) the seasonal pattern of the ecosystem responses and (2) the source of variability in carbon flux. We investigated to what extent and at which temporal scales, climate variability and changes in ecosystem functional properties determined the IAV of carbon balance. A semi-empirical model (Lasslop et al., 2010b) was applied to estimate seasonal and interannual variation in the ecosystem functional properties. We tested the hypothesis that long-term ecosystem carbon dynamics are mostly driven by changes in ecosystem functional properties, despite the significant role of climate variability.

2 Material and methods

2.1 Site description

Field measurements were taken at the Euroflux network station Sorø on Zealand, Denmark (55°29′ N, 11°38′ E). A brief description of the site and measurements follows, for detailed information about the instrumentation, see Pilegaard et al. (2003); soil and vegetation (Ladekarl, 2001; Pilegaard et al., 2001); fetch and footprint analysis (Dellwik and Jensen, 2000, 2005; Göckede et al., 2008; Pilegaard et al., 2011). Mean annual temperature during the measurement period was 8.5 °C and mean annual precipitation sum was 564 mm. The dominant tree species is European beech (*Fagus sylvatica*) with approximately 20 % conifers, mainly Norway spruce (*Picea abies*) and European larch (*Larix decidua*). The stand around the flux tower is about 90 years old. The average tree height in the stand was 28 m and the diameter at breast height was 41 cm in 2010. Soils are classified as Alfisols or Mollisols (depending on the base saturation) with 10–40 cm deep organic layers. Leaf area index peaks at 4–5 m^{-2} m^{-2} and no significant trend was observed in 2000–2009 (Pilegaard et al., 2011).

2.2 Flux measurements and partitioning

Thirteen years (1997–2009) of continuous half-hourly measurements of NEE and climate data were used in the present analysis. The flux measurements were conducted at 43 m above the canopy and the data processing followed the standard procedure of Aubient et al. (2000) as described in Pilegaard et al. (2011). Spectral corrections were applied to the flux data according to Ibrom et al. (2007). The fluxes were filtered at low turbulent mixing at stable stratification when the friction velocity (u_*) was lower than $0.1\,\mathrm{m\,s^{-1}}$. Correction for CO_2 storages below the measurement height were applied (Pilegaard et al., 2011). Partitioning of the NEE into the two component fluxes GPP and TER was based on the Q_{10} function. TER was estimated based on nighttime data and extrapolated into daytime flux according to the following equation:

$$\mathrm{TER} = r_\mathrm{b} Q_{10}^{\frac{T_S - T_0}{10}} \tag{1}$$

where T_0 is the reference soil temperature at 2 cm depth (0 °C); r_b is the base respiration at T_0; T_s is the measured soil temperature at 2 cm and Q_{10} is the temperature sensitivity parameter and set to a constant value of 2. Parameter estimation was conducted for every night and the estimated function was used to extrapolate the nighttime ecosystem respiration over daytime based on soil temperature measured at daytime. GPP was subsequently calculated as:

$$\mathrm{GPP} = \mathrm{TER} - \mathrm{NEE} \tag{2}$$

2.3 Correlation analysis

To evaluate the ecosystem response to climatic variability, correlation analysis was first performed between the annual carbon flux integrals (annual sums of NEE, GPP and TER) and the mean annual climate variables, i.e. air temperature T_air, global radiation R_g, volumetric soil water content SWC in the top soil, and precipitation PPT, using data from 13 years with all possible combinations. In the second step, the same correlation analysis was applied at sub-annual time scale with a 30 day moving window. Pearson's correlation coefficients were calculated between periodical flux integrals (30 day sum of the GPP and TER) and mean periodical climate variables from each of the 13 years. This was done for every day of the year (DOY, index i) resulting in a time series of correlation coefficients (r_i):

$$r_\mathrm{i} = \frac{\mathrm{cov}(F_\mathrm{i}, \overline{C_\mathrm{i}})}{\sigma F_\mathrm{i} \sigma \overline{C_\mathrm{i}}} \tag{3}$$

where F_i and $\overline{C_\mathrm{i}}$ was the sum of the carbon flux (NEE, GPP or TER) and average climate variable, respectively, within a moving time window from DOY i-14 to i+15 in the 13 years. The resulting time series of correlation coefficients were a representation of the seasonality of interannual variability, i.e. relating the interannual variability of the carbon flux with a potential climatic driver in a certain period of a year. This enabled the analysis of interannual variability at sub annual time scales.

2.4 Model description and parameter estimation

A rectangular hyperbolic light response curve (Falge et al., 2001) was fitted to daytime NEE, with modifications to account for the changes in the temperature sensitivity of TER (Lloyd and Taylor, 1994). The effects of air humidity over photosynthesis were accounted according to Körner (1995). The model is described in Eq. (3 and 4).

$$\mathrm{NEE} = -\frac{\alpha\beta R_\mathrm{g}}{\alpha R_\mathrm{g} + \beta} + r_\mathrm{b} \exp\left(E_0\left(\frac{1}{T_\mathrm{ref} - T_0} - \frac{1}{T_\mathrm{air} - T_0}\right)\right) \tag{4}$$

where T_air is the air temperature; T_0 (°C) is a constant at $-46.02\,^\circ\mathrm{C}$; α ($\mu\mathrm{mol\,C\,J^{-1}}$) is the light use efficiency; β ($\mu\mathrm{mol\,C\,m^{-2}\,s^{-1}}$) is the maximum photosynthetic capacity at light saturation; R_g ($\mathrm{W\,m^{-2}}$) is the global radiation; r_b ($\mu\mathrm{mol\,C\,m^{-2}\,s^{-1}}$) is the base respiration at reference temperature ($T_\mathrm{ref} = 15\,^\circ\mathrm{C}$); E_0 is a scaling parameter for the temperature sensitivity. E_0 was allowed to vary across different seasons as it represents the changes in substrate quality; contribution of above and belowground respiration; and also possible changes in the microbial communities.

$$\beta = \begin{cases} \beta = \beta_0, \mathrm{VPD} < \mathrm{VPD}_0 \\ \beta = \beta_0 \exp(-k(\mathrm{VPD} - \mathrm{VPD}_0)), \mathrm{VPD} > \mathrm{VPD}_0 \end{cases} \tag{5}$$

where k is a scaling parameter estimating the effects of VPD on the maximum photosynthetic capacity and VPD_0 is a threshold value set as 10 hPa, above which the stomatal conductance tends to reduce. The parameter α, β, r_b and k were estimated based on daytime data every two days, with a 4 day moving window. E_0 was derived from nighttime data every 2 days using a 12 day window. Parameter estimation was conducted by minimizing the weighted least squares cost function (Richardson and Hollinger, 2005) and the half-hourly fluxes were computed using distance weighted average parameter sets; details are described in Lasslop et al. (2010b).

2.5 Distinguishing the direct response from biotic changes

By prescription of the parameter time series of one year to all the other years and comparing the differences in the modelled fluxes, the effects of climate forcing on the carbon fluxes can be investigated, vice versa for the effects of the parameters. After Richardson et al. (2007), model simulations with fixed climate (using climate data of one year for all other year) and fixed parameters (using parameter dataset of one year for all other years) were performed, resulting in a 13 × 13 matrix of model predictions. In each cell of this matrix, the simulated results contained 17 520 half-hourly data points, which was further aggregated by day, week, month, season and year for statistical analysis. Therefore, the datasets in each column represented the modelled fluxes with fixed climate using climate data of a particular year i ($F_{\mathrm{clifix,i}}$) and the datasets in each row represented the modelled fluxes with fixed parameter using parameter time series of year i ($F_{\mathrm{parfix,i}}$). The diagonal of the matrix represents the original modelled fluxes (F_{original}). The differences between F_{original} and F_{clifix} yield the variability that is driven by the climate while the differences between F_{original} and F_{parfix} yield the variability that is driven by the model parameters. We applied a sum of squared error approach to distinguish the relative effect of climate and model parameters on the IAV in NEE, GPP and TER at multiple time scales ranging from daily to yearly. The IAV in the carbon fluxes explained by climate variability (E_{cli}) was quantified by following equation:

$$E_{\text{cli}} = \overline{\sigma(F_{\text{original}} - F_{\text{clifix,i}})} \Big/ \left(\overline{\sigma(F_{\text{original}} - F_{\text{clifix,i}})} + \overline{\sigma(F_{\text{original}} - F_{\text{parfix,i}})}\right) \tag{6}$$

3 Results

3.1 Interannual variability in carbon fluxes and climate variables

Variation in NEE and the climate variables were analyzed at both sub-annual (daily value smoothed with a 30-day moving average) and annual time scales (Fig. 1). The variability was displayed as fluctuations (around the mean) relative to the standard deviations, i.e. $(\chi - \overline{\chi})/\sigma\chi$, in a certain time window over the 13 years. This presentation enabled a standardized comparison of the anomalies in both carbon fluxes and climate variables with their interannual variability, during a particular period of a year. In 1998, the forest was a source of carbon (Table 1) where the deviation of NEE from the 13-year annual mean was about 2 standard deviations (SD) above average (more positive means less uptake). Following this, a trend of increasing carbon uptake in the forest was observed, manifested with the higher uptake during the latest years 2008–2009 when the NEE was almost 2 SD below average (Fig. 1). Except for these years, the annual NEE deviations were less than 1 SD. Generally, there was a tendency from above average towards below average except in 2003 and 2006, when the forest appeared to have a reduced rate of carbon uptake.

Carbon uptake was less than average in almost all periods of the years from 1997 to 1999, except in autumn 1999 when the uptake was about 1SD above average. In 2000–2006 the NEE anomaly fluctuated remarkably within each year, ranging from 2 SD above average in winter 2000 to 2 SD below average in autumn 2005. Regardless

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the high variability at short time scales, these NEE anomalies tended to compensate each other, resulting in the annual flux close to the 13 year average. From 2007 to 2009, NEE was continuously below average with higher carbon uptake except in two short periods of summer 2007 and the beginning of 2008.

The mean annual air temperature of the only source year 1998 was the lowest over the 13 year period, with more than 1 SD below average. Meanwhile, overcast weather (lowest incoming radiation) and the slightly higher than average precipitation kept the soil water content at 1 SD above average. The opposite conditions prevailed in 2008 compared to 1998. Higher radiation (almost 2 SD above average) was accompanied with higher air temperature and the evaporative demand which significantly reduced the soil water content. Note the measurement of soil water content in 2008–2009 was slightly different from the previous years due to breakdown of the TDR system. The new installation was at the same location but in a shallower soil horizon (5 instead of 10 cm previously).

3.2 Climatic control of the interannual variability in the carbon fluxes

The correlation analysis showed the connection between the interannual variability of the component carbon fluxes and certain climate variables. On the annual time scale, NEE (defined as uptake negative) was highly correlated with GPP (defined as uptake positive) ($r = -0.7$, $p < 0.01$) but not with TER (defined as release positive) (Table 2). TER, on the other hand, was highly correlated with GPP ($r = 0.65$, $p < 0.05$). Apart from soil water content, which was positively correlated with precipitation (0.76, $p < 0.01$) and negatively correlated with radiation (–0.77, $p < 0.01$), there were no significant correlations between other climate variables. Global radiation and soil water content were negatively (–0.73, $p < 0.01$) and positively (0.62, $p < 0.05$) correlated with NEE, respectively. Soil water content was low at high R_g and therefore correlated with NEE. Surprisingly, none of the climate variables showed a significant correlation with the component fluxes, GPP and TER.

In contrast to the analysis at annual time scale, carbon fluxes were clearly correlated with climatic variables at shorter time scales (Fig. 2). These correlations indicate different phases of the annual course when interannual variability of the C fluxes was tightly coupled to certain climate variables. GPP was highly correlated with T_{air} ($r > 0.69$, $p < 0.01$) throughout the entire year except during part of the summer (Fig. 2a), when soil water content controlled the interannual variability. The correlation between GPP and T_{air} was highest ($r > 0.8$, $p < 0.01$) around leaf flush in April and senescence in October, indicating that the onset of the phenological phases and leaf development was temperature controlled. Radiation was also positively correlated with GPP during winter, spring and autumn. The correlation decreased after leaf senescence but returned in November, representing the coniferous photosynthesis. Over a large part of the year, the correlation between GPP and SWC was not significant, possibly because the deep rooting system could ensure water supply even when the water in the top soil was depleted. Nevertheless, the trend of increasing correlation during the summer was obvious and the value peaked in Aug–Sep. The seasonality of temperature regulation on TER was similar to GPP (Fig. 2b). Correlation was positive during the spring, autumn and winter but turned negative during summer when low SWC seemed to inhibit TER. Similar to the analysis at annual time scale, TER and GPP were significantly correlated during large parts of spring and summer. Because the climate variables were also inter correlated (Fig. 2c), the attribution of the interannual C flux variability to specific climatic variables was sometimes difficult, especially for T_{air} and R_{g}, which were significantly correlated during spring and summer. R_{g} and SWC were in general negatively correlated and most significantly in June and October.

The comparison of temporal variability of climate variables and carbon fluxes (Fig. 3) during the average and particular years (1998 and 2008, minimum and maximum in annual NEE) illustrated the seasonal pattern of climate control based on the correlation analysis (Fig. 2). While T_{air} was low during 1998 summer (Fig. 3a), higher than average SWC (Fig. 3c) was accompanied with higher than average TER (Fig. 3f). Following the summer, low T_{air} and R_{g} (Fig. 3a and b) led to lower GPP during the autumn (Fig. 3e).

Lower cumulative GPP (Fig. 3h) and higher cumulative TER (Fig. 3i) resulted in 1998 the only source year of carbon within the 13 years (Fig. 3i). In contrast, the summer in 2008 was in general dry but featured a rewetting period around August, the effect of moisture was also apparent in TER however with a smaller magnitude compared with 1998. TER significantly increased after the rewetting but only reached the average level. GPP was higher than average during the early summer due to the particularly high radiation. In 2008 autumn, GPP was also higher than average although the radiation and temperature were slightly above the 13-year average. With higher cumulative GPP and lower cumulative TER, the annual carbon uptake of 2008 was the highest within the 13 year period.

3.3 Estimated parameter time series and model predictions

The estimated parameter time series varied between years. During leafed period, mean light use efficiency was highest in 2000 (0.123 µmol C J^{-1}) and lowest in 2003 (0.093 µmol C J^{-1}). Maximum photosynthetic capacity (β) ranged between 37.1 (2002) to 48.8 (2005) µmol C m^{-2} s^{-1}. For TER related parameters, annual mean base respiration ranged from 4.7 (2002) to 6.0 (1998) µmol C m^{-2} s^{-1}. The temperature sensitivity parameter (E0) ranged between 135.1 (2002) to 191.3 (2008). The seasonal variation in the parameters was higher than the variation in the annual means (Fig. 4). Light use efficiency and maximum photosynthetic capacity (Fig. 4a) were approximately one order of magnitude higher during the growing season than in winter. The sensitivity of VPD limitation (k) only affected the fluxes during leafed period, when the VPD is above certain threshold. Therefore, instead of presenting the ensemble mean of the all the 13 years, data from 1998 (wet year) and 2003 (dry year) were presented as examples (Fig. 4b). In 1998, k was highest around 1.5 during autumn whereas in 2003, it was highest around 1.8 in early summer. The seasonal variation in the TER related parameter was slightly lower (Fig. 4c). On average, r_b ranged from 2.7 to 9.2 µmol C m^{-2} s^{-1}. E_0 ranged from 118 to 265, with the highest values found in autumn.

Based on the estimated parameter time series and climate data of each year, the model prediction (Eq. 3) explained on average 83 % of the variance in the annual half-hourly measured (non gap-filled) NEE (Table 1). Root mean squared error (RMSE) was highest in 1999 (3.68 µmol C m^{-2} s^{-1}) and lowest in 2002 (2.66 µmol C m^{-2} s^{-1}). Mean absolute error (MAE) ranged from 0.02 to 0.19 µmol C m^{-2} s^{-1} in 1997 and 2007 respectively. At an annual time scale, the correlation between gap-filled and modelled NEE was 0.92. The modelled NEE was lowest in 2008 (–392 g C m^{-2} yr^{-1}) and highest in 1998 (55 g C m^{-2} yr^{-1}) which agreed with the gap-filled fluxes (Table 1). The discrepancy between gap-filled and modelled NEE was exceptionally large in 2003–2005, as up to 25 % of the data are missing in these years. While the annual NEE time series were gap-filled (Pilegaard et al., 2011), the corresponding gaps in the parameter time series were filled based on linear interpolation between the two adjacent values. Both these uncertainties contributed to this discrepancy. IAV in the modelled NEE (1 SD = 142 g C m^{-2} yr^{-1}) was 37 % higher than the measured NEE (1 SD = 104 g C m^{-2} yr^{-1}). It was also higher than the IAV in the modelled GPP (1 SD = 126 g C m^{-2} yr^{-1}) and TER (1 SD = 117 g C m^{-2} yr^{-1}).

3.4 Source of interannual variability in the carbon fluxes

Interannual variation in the modelled NEE differed when either the parameters or the climate variables were fixed (Fig. 5). When the parameters were fixed, therefore assuming the ecosystem status during the 13 years was constant (Fig. 5b), the modelled fluxes NEE_{parfix} ranged between –294 g C m^{-2} yr^{-1} in 2009 and –92 g C m^{-2} yr^{-1} in 2007. When the climate time series was fixed (Fig. 5c), NEE_{clifix} ranged between 19 g C m^{-2} yr^{-1} in 1998 and –367 g C m^{-2} yr^{-1} in 2007. The IAV in the originally modelled fluxes $NEE_{original}$ (Fig. 5a) was better reproduced when the changes in the parameter time series were included. The correlation between the $NEE_{original}$ and NEE_{clifix} was 0.89 ($p < 0.01$). In contrast, correlation between the NEE_{parfix} and $NEE_{original}$ was not significant. The differences in these modelled fluxes represent the climate and parameter effects; these effects can be interpreted as the influence of changes in climate and ecosystem functional properties, respectively.

The originally modelled annual GPP (13 year mean = $1845\,\mathrm{g\,C\,m^{-2}\,yr^{-1}}$), TER ($1646\,\mathrm{g\,C\,m^{-2}\,yr^{-1}}$), and NEE ($-199\,\mathrm{g\,C\,m^{-2}\,yr^{-1}}$) were used as base lines to evaluate the relative effects of climate and parameters in each year (Fig. 6). Deviation of the $\mathrm{GPP_{clifix}}$ and $\mathrm{GPP_{parfix}}$ from these references (Fig. 6a) suggested that the climate effect ranged between $-78\,\mathrm{g\,C\,m^{-2}\,yr^{-1}}$ (2000) to $+114\,\mathrm{g\,C\,m^{-2}\,yr^{-1}}$ (2009). The parameter effects on GPP were stronger and ranged between $-203\,\mathrm{g\,C\,m^{-2}\,yr^{-1}}$ (1997) and $+257\,\mathrm{g\,C\,m^{-2}\,yr^{-1}}$ (2004). The climate effect on TER was slightly lower than that on GPP (Fig. 6b), ranged between $+69\,\mathrm{g\,C\,m^{-2}\,yr^{-1}}$ (2006) to $-62\,\mathrm{g\,C\,m^{-2}\,yr^{-1}}$ (1998). The parameter effect on TER was most positive in 1998 ($+286\,\mathrm{g\,C\,m^{-2}\,yr^{-1}}$) and most negative in 2002 ($-205\,\mathrm{g\,C\,m^{-2}\,yr^{-1}}$). In general, the climate effects on GPP and TER compensated for each other, resulting in a reduced effect on NEE. In contrast, in 1999, 2000 and 2006, the direction of these two effects was consistent and led to an amplified effect on NEE. Similarly, the parameter year effects on GPP and TER were both favourable for carbon uptake in 2005, 2007 and 2009 and for carbon loss in 1999. The combined effects of parameter and climate on the IAV in NEE (Fig. 6c) agreed well with the observations (Fig. 1a).

Based on the 13 × 13 matrix of model predictions, where the parameter and climate time series of each year were applied factorially, analysis of the relative impacts of climate and parameters indicated that, up to 77 % of the variance in NEE was attributable to the interannual variation in the parameter time series (Fig. 7). GPP was more sensitive to variation in climate than TER. In general, the percentage of the total variance in the carbon flux caused by climate variability increased as the integrated time period reduced. At a daily time scale, climate variability accounted for more than 65 % of the variation in GPP and NEE. The estimated effect of climate variability on TER was very low (25 %), even at the daily time scale.

4 Discussion

4.1 Climate variability and average climate change

The correlation analysis between carbon fluxes and climatic variables revealed that the variations in the mean annual climate could not directly explain the IAV in the ecosystem carbon balance. Global radiation and soil water content were significantly correlated with NEE (Table 2). However, contrary to our expectations, neither R_g nor SWC were significantly correlated with the gross photosynthesis or total ecosystem respiration, i.e. the processes that drive NEE. Ecosystem respiration was low in years with higher radiation ($r = -0.44$, $p > 0.05$), which might have strengthened the correlation between R_g and NEE. SWC was low in years with high radiation and was thus also correlated with NEE. Therefore, despite comparably high correlation coefficients, these correlations do not represent direct cause-effect relationships between mean annual climate variables and NEE. Rather, they are the result of the combination of the various controlling mechanisms in different seasons, as illustrated by the correlation analysis at short time scales.

At shorter time scales, the ecosystem response to climate variability significantly increased. For more than 80 % of the year, the carbon flux was strongly controlled ($r > 0.55$, $p < 0.05$) by at least one of the investigated climate variable (Fig. 2). Considering the variability of all climate variables and the non-linear ecosystem response, the modelling experiment showed that climate variability accounted for 67 % of the IAV in NEE at the daily time scale (Fig. 8). As the time of integration increased and the variability in the climate was averaged over a longer period, its impact on carbon fluxes was reduced. Apart from the high correlation throughout the year, the dominating climate variable for carbon fluxes varied in different seasons (Fig. 2). For example, the response of GPP to temperature was generally positive, but became negative during summer due to the confounding effects of low soil water availability. This differs from boreal ecosystems where temperature was the most limiting factor during summer (Vesala et al., 2010). The negative correlation between GPP and temperature was not a causal relationship but was the result of the coincidence between climate variables (Fig. 2c); this made the identification of the fundamental underlying mechanism difficult. Consequently, climate variability affected the net ecosystem carbon balance through the aggregation of these two opposing fluxes, GPP and TER. Depending on the response (positive or negative) and sensitivity of GPP and TER to changes in climate variables, the climatic impact on NEE could either be amplified or attenuated, or even the direction of the effect reversed. In Fig. 6 we demonstrated that in most years, the climate effect on GPP and TER tended to compensate for each other, resulting in a reduced effect on NEE.

The significant seasonality of the ecosystem responses to climatic variability demonstrated the importance of the seasonal distribution of the changing climate on future ecosystem carbon balances. Our results show that this Beech forest will be sensitive to increases in summer drought. Altered precipitation patterns, i.e. increased rainfall variability rather than changes in total precipitation are likely to affect ecosystem carbon balances in the future (Knapp et al., 2002). The average climate change will be accompanied by increased variability and weather extremes (Easterling et al., 2000a, b). Climate change projections for Denmark suggest an increase in precipitation will occur, but mainly during winter, while the likelihood of summer droughts will increase (Christensen and Christensen, 2007). Our results suggest that in addition to the changes in average climate, increased climatic variability could alter the ecosystem carbon balance more strongly, as the climate anomalies are projected to take place predominantly during biologically active periods.

4.2 Magnitude and uncertainty of the estimated impact of functional change

The 13 year trend of increasing carbon uptake was found to be more strongly driven by the aggregated effect of parameters than the climatic factors. In addition to the changes in the maximum photosynthetic capacity and the carbon uptake period (Pilegaard et al., 2011), we found other photosynthesis and respiration related parameters also changed in different years and indirectly affected the ecosystem carbon balance. The estimated impact of functional change at Sorø was higher than at other sites (Teklemariam et al., 2010; Richardson et al., 2007; Hui et al., 2003). One possible reason is the different type and structure of the ecosystem. The impact of the functional change was decreasing in the order: deciduous forest (this study), mixed forest (Richardson et al., 2007), conifer forest (Hui et al., 2003) and peatland (Teklemariam et al., 2010), implying a difference in the resistance of these ecosystems towards environmental change and disturbance. Cross-site studies on IAV in the ecosystem carbon balance also found that deciduous forests tend to be more sensitive than evergreen conifer forests to climate variability (Yuan et al., 2009) and phenological transitions (Richardson et al., 2010). These differences in the adaptive capacity to changing climate between deciduous and evergreen forests may drive shifts in the composition within mixed forests (Richardson et al., 2010).

The differences in the estimated magnitude of functional changes might also stem from the method applied. In this study, we used a moving window approach for parameter estimation, which significantly improved the model prediction ($r^2 = 83\,\%$) and also increased the proportion of variance that is attributed to the parameter changes, compared to Richardson et al. (2007), where the model was more complex but the parameters were kept constant within a year. One clear advantage of our approach is that it allows for seasonal variability of the model parameters. Therefore, the IAV in the leaf flush and senescence observed at Sorø (Pilegaard et al., 2011), can be well represented by the high resolution parameter time series. Jeong et al. (2011) observed similar phenological shifts over the Northern hemisphere, showing that sub-annual parameter variability is common in many ecosystems. Therefore, our method could be potentially applied at other flux sites to evaluate the magnitude of functional change over larger spatial scale.

The estimated impact of functional change is not without uncertainties, mainly due to the assumption that functional change is solely represented by the changes in model parameters. This assumption is challenged by the simplicity of the model structure, e.g., the temperature regulation of GPP and the SWC regulation of TER were not explicitly specified in the model structure. Alternatively, Richardson et al. (2007) applied a set of environmental scalar functions to adjust the fluxes under sub-optimal conditions, which was then used for parameter estimation. In this way the estimated "potential" parameters should be independent from the climate. In our study, instead of using environmental scalar functions, the parameters of the empirical model were allowed to vary throughout the year by making the parameter estimations within moving windows. This approach is more flexible and adaptive rather than relying on the validity of scalar functions. However, this approach might be too flexible and variations in the meteorological conditions might propagate into variations of the parameter estimates, if not represented in the simple empirical model. We assessed the uncertainties in the influence of temperature on GPP (which is not explicitly included in the model) by plotting the simulated daily GPP at light saturation ($R_g = 1000\,\mathrm{W\,m^{-2}}$) with T_{air} (Fig. 8a). A clear relationship between T_{air} and the GPP-related parameters was found when the whole year data was used, however, during the period when the canopy was fully developed and LAI was relatively constant (May–Sep), no significant relationship between T_{air} and the GPP was found. This indicates that although we did not explicitly account for the temperature effect on GPP in the model, it was partly represented by the model due to the cross correlation between temperature and VPD or temperature and radiation. Therefore the large part of the correlation between temperature and parameters, when using the whole data set, are derived from functional changes that were either caused by or coincided with temperature. In contrast, the TER-related parameters were not completely independent from SWC, especially during the growing season (Fig. 8b). Approximately 16 % of the parameter effect on TER could be attributed to variation in SWC (Fig. 8b). We further correlated the parameter effects for TER (black bar in Fig. 6b) with mean annual SWC ($r = 0.38$, $p > 0.05$) and mean SWC in spring ($r = 0.08$, $p > 0.05$), summer ($r = 0.36$, $p > 0.05$), autumn ($r = 0.49$, $p > 0.05$) and winter ($r = 0.01$, $p > 0.05$). Although none of these correlations appeared significant, the results indicated that part of the SWC effect on TER has been propagated into the parameters, which has led to a small overestimation of functional change.

4.3 GPP as a driver of the IAV in NEE

Interannual variation in the NEE in this beech forest was mostly driven by GPP whereas TER had relatively less influence. This was similar to two deciduous forests in both boreal and temperate zones (Barr et al., 2002). However, the results of these two studies differed from the conclusion of a cross-site synthesis of 15 European forests (Valentini et al., 2000) where respiration was found to determine the spatial variability in ecosystem carbon balance. According to this synthesis, net carbon uptake decreased significantly with increasing latitude, whereas total ecosystem respiration increased and gross photosynthesis tended to be independent of the latitude. These different findings based on site specific study and cross-site synthesis indicated that although TER tended to vary significantly and dominate the ecosystem carbon balance over large spatial scale, its influence on the temporal variability in NEE was much smaller at site level. For deciduous forests at middle and high latitudes, the variability in GPP was much stronger and largely controlled the interannual variation in the ecosystem carbon balance.

TER was highly correlated with GPP, both at annual and sub-annual time scales. It is still under debate whether this correlation could be artificial because GPP was calculated from TER and NEE (Vickers et al., 2009). Lasslop et al. (2010a), however, suggested that only the error in TER that directly propagates into GPP can cause spurious correlation, a large part of the variability of TER is still independent from GPP, and thus the correlation between GPP and TER was rather real than spurious. This suggestion can be supported by using a TER estimate derived from a fit of a respiration model to nighttime data in combination with a GPP estimate derived using a light response curve fit to daytime data. In this case the errors in one flux component cannot directly propagate to the other and the correlation remains high (Lasslop et al. 2010b). A more likely explanation for the high correlation is partly the covariance of the main drivers of photosynthesis and respiration, e.g. temperature and radiation. From the physiological perspective the correlation could be an effect of substrate availability on autotrophic (plant activity, i.e. growth respiration and reserve metabolism) and heterotrophic respiration (root exudates and litter fall). This interpretation is supported by an increasing number of experimental studies, such as tree girdling studies (Högberg et al., 2001) or direct and quasi parallel measurement of GPP and TER during daytime with ecosystem chambers in shrublands (Larsen et al., 2007).

4.4 Possible causes of functional changes

The present study has focused on the consequence of ecosystem functional changes, rather than their causes. It is difficult to investigate the causes of functional change with the available data because of (1) the non-linearity of the ecosystem response (Zhou et al., 2008); (2) different pathways, as more than one type of climate anomaly can lead to changes in the ecosystem parameters (Richardson et al., 2007); and (3) the different lengths of the lagged responses. Changes in LAI due to water stress or other climatic disturbance could be one of the key issues for the functional change (Barr et al., 2004), however no significant changes in the LAI were observed (Pilegaard et al., 2011). Increased leaf nitrogen content could explain this phenomenon (Leuning et al., 1995); however supporting measurements are not available. Other potential influential factors could be non-structural carbohydrate reserves (Hoch et al., 2003) or transient litter pools. Vesala et al. (2010) indicated the transient pools of the litter on the forest floor could be a cause for the Interannual variation in the base respiration. To better understand these indirect and lagged processes, more targeted observations and data are needed.

4.5 Implication for mechanistic models

The results of this study suggest that projection of future carbon balance of terrestrial ecosystems will be significantly improved if the biotic responses to climate variability and thus functional change could be properly incorporated into mechanistic models. Migliavacca et al. (2011) demonstrated that the spatiotemporal variability in ecosystem respiration can be better modelled when the dynamics in the biotic factors are taken into account. Modelling IAV in carbon balance has proven difficult (Siqueira et al., 2006). One important reason is that most parameters are usually kept constant, for example, in global models, parameters are usually static for plant functional types (Krinner, 2005; Sitch et al., 2003). Increasing model complexity by adding processes that enable change in ecosystem state (e.g. nitrogen cycling or dynamics in the microbial community) could possibly improve the situation. However, this could lead to model over-parameterization and increase the demand for validation data, thus limiting model application at large spatial scales. Nevertheless, site level studies clearly show the necessity for further development of these functional change modules. Thus, using an alternative approach by establishing empirical functional relationships between parameters and independent variables and subsequently embedding them in the model could be an intermediate solution. Therefore, combining experimental studies, empirical and mechanistic modelling could elucidate the importance of functional changes when simulating future terrestrial carbon budgets and potentially improve the prognostic capacity of the ecosystem models.

5 Conclusions

The process-oriented empirical analysis in this study enabled interpreting interannual variability in net ecosystem flux through its component fluxes, GPP, TER and their responses to both climate variability and changing ecosystem functional properties. The estimated impacts of climate variability and functional change on the processes of carbon cycling depended on the temporal scales. Changes in the climate had significantly stronger control on the carbon fluxes at short time scales but this impact reduced as the time integral increased. On longer temporal scale, the effect of biotic factors became progressively larger and appeared to dominate the interannual variability in the ecosystem carbon balance. We found that both the photosynthesis and respiration related parameters changed between years and were responsible for the observed trend of increasing carbon uptake, supplementing the previous results from this site. We advocate applying the proposed method in other sites with pronounced functional seasonality to explore ecosystem behavior across different functional types. The simple semi-empirical model could be improved by incorporating the influence of soil water content on TER. While the importance of functional change was clearly demonstrated, further investigation of the cause of functional change could contribute to the development of mechanistic models and hence reduce the uncertainty in long term projections of ecosystem carbon balance.

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References

Aubinet, M., Grelle, A., Ibrom, A., Rannik, S., Moncrieff, J., Foken, T., Kowalski, A., Martin, P., Berbigier, P., and Bernhofer, C.: Estimates of the annual net carbon and water exchange of forests: the EUROFLUX methodology, Adv. Ecol. Res., 30, 113–175, 2000.

Baldocchi, D.: Assessing the eddy covariance technique for evaluating carbon dioxide exchange rates of ecosystems: past, present and future, Glob. Change Biol., 9, 479–492, 2003.

Barr, A., Griffis, T., Black, T., Lee, X., Staebler, R., Fuentes, J., Chen, Z., and Morgenstern, K.: Comparing the carbon budgets of boreal and temperate deciduous forest stands, Can. J. Forest Res., 32, 813–822, 2002.

Barr, A., Black, T., Hogg, E., Kljun, N., Morgenstern, K., and Nesic, Z.: Interannual variability in the leaf area index of a boreal aspen-hazelnut forest in relation to net ecosystem production, Agr. Forest Meteorol., 126, 237–255, 2004.

Barr, A., Black, T., Hogg, E., Griffis, T., Morgenstern, K., Kljun, N., Theede, A., and Nesic, Z.: Climatic controls on the carbon and water balances of a boreal aspen forest, 1994–2003, Glob. Change Biol., 13, 561–576, 2007.

Beer, C., Reichstein, M., Tomelleri, E., Ciais, P., Jung, M., Carvalhais, N., Rodenbeck, C., Arain, M. A., Baldocchi, D., Bonan, G. B., Bondeau, A., Cescatti, A., Lasslop, G., Lindroth, A., Lomas, M., Luyssaert, S., Margolis, H., Oleson, K. W., Roupsard, O., Veenendaal, E., Viovy, N., Williams, C., Woodward, F. I., and Papale, D.: Terrestrial Gross Carbon Dioxide Uptake: Global Distribution and Covariation with Climate, Science, 329, 834–838, doi:10.1126/science.1184984, 2010.

Black, T., Chen, W., Barr, A., Arain, M., Chen, Z., Nesic, Z., Hogg, E., Neumann, H., and Yang, P.: Increased carbon sequestration by a boreal deciduous forest in years with a warm spring, Geophys. Res. Lett., 27, 1271–1274, 2000.

Chen, W., Black, T., Yang, P., Barr, A., Neumann, H., Nesic, Z., Blanken, P., Novak, M., Eley, J., and Ketler, R.: Effects of climatic variability on the annual carbon sequestration by a boreal aspen forest, Glob. Change Biol., 5, 41–53, 1999.

Christensen, J. H. and Christensen, O. B.: A summary of the PRUDENCE model projections of changes in European climate by the end of this century, Climatic Change, 81, 7–30, 2007.

Churkina, G., Schimel, D., Braswell, B., and Xiao, X.: Spatial analysis of growing season length control over net ecosystem exchange, Glob. Change Biol., 11, 1777–1787, 2005.

Dellwik, E. and Jensen, N.: Internal equilibrium layer growth over forest, Theor. Appl. Climatol., 66, 173–184, 2000.

Dellwik, E. and Jensen, N. O.: Flux-profile relationships over a fetch limited beech forest, Bound.-Lay. Meteorol., 115, 179–204, 2005.

Falge, E., Baldocchi, D., Olson, R., 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., Lai, C. T., 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., and Wofsy, S.: Gap filling strategies for defensible annual sums of net ecosystem exchange, Agr. Forest Meteorol., 107, 43–69, doi:10.1016/s0168-1923(00)00225-2, 2001.

Friedlingstein, P., Houghton, R., Marland, G., Hackler, J., Boden, T., Conway, T., Canadell, J., Raupach, M., Ciais, P., and Le Quéré, C.: Update on CO2 emissions, Nature Geosci., 3, 811–812, 2010.

Göckede, M., Foken, T., Aubinet, M., Aurela, M., Banza, J., Bernhofer, C., Bonnefond, J. M., Brunet, Y., Carrara, A., Clement, R., Dellwik, E., Elbers, J., Eugster, W., Fuhrer, J., Granier, A., Grünwald, T., Heinesch, B., Janssens, I. A., Knohl, A., Koeble, R., Laurila, T., Longdoz, B., Manca, G., Marek, M., Markkanen, T., Mateus, J., Matteucci, G., Mauder, M., Migliavacca, M., Minerbi, S., Moncrieff, J., Montagnani, L., Moors, E., Ourcival, J.-M., Papale, D., Pereira, J., Pilegaard, K., Pita, G., Rambal, S., Rebmann, C., Rodrigues, A., Rotenberg, E., Sanz, M. J., Sedlak, P., Seufert, G., Siebicke, L., Soussana, J. F., Valentini, R., Vesala, T., Verbeeck, H., and Yakir, D.: Quality control of CarboEurope flux data Part 1: Coupling footprint analyses with flux data quality assessment to evaluate sites in forest ecosystems, Biogeosciences, 5, 433–450, doi:10.5194/bg-5-433-2008, 2008.

Heimann, M. and Reichstein, M.: Terrestrial ecosystem carbon dynamics and climate feedbacks, Nature, 451, 289–292, 2008.

Hoch, G., Richter, A., and Körner, C.: Non structural carbon compounds in temperate forest trees, Plant. Cell. Environ., 26, 1067–1081, 2003.

Hollinger, D., Aber, J., Dail, B., Davidson, E., Goltz, S., Hughes, H., Leclerc, M., Lee, J., Richardson, A., and Rodrigues, C.: Spatial and temporal variability in forest–atmosphere CO2 exchange, Glob. Change Biol., 10, 1689–1706, 2004.

Hu, J., Moore, D., Burns, S., and Monson, R.: Longer growing seasons lead to less carbon sequestration by a subalpine forest, Glob. Change Biol., 16, 771–783, 2010.

Hui, D., Luo, Y., and Katul, G.: Partitioning interannual variability in net ecosystem exchange between climatic variability and functional change, Tree Physiol., 23, 433-442, 2003.

Högberg, P., Nordgren, A., Buchmann, N., Taylor, A. F. S., Ekblad, A., Högberg, M. N., Nyberg, G., Ottosson-Löfvenius, M., and Read, D. J.: Large-scale forest girdling shows that current photosynthesis drives soil respiration, Nature, 411, 789–792, 2001.

Ibrom, A., Jarvis, P. G., Clement, R., Morgenstern, K., Oltchev, A., Medlyn, B. E., Wang, Y. P., Wingate, L., Moncrieff, J. B., and Gravenhorst, G.: A comparative analysis of simulated and observed photosynthetic CO2 uptake in two coniferous forest canopies, Tree Physiol., 26, 845-864, 2006.

Ibrom, A., Dellwik, E., Flyvbjerg, H., Jensen, N. O., and Pilegaard, K.: Strong low-pass filtering effects on water vapour flux measurements with closed-path eddy correlation systems, Agr. Forest Meteorol., 147, 140–156, 2007.

Jeong, S.-J., Ho, C.-H., Gim, H.-J., and Brown, M. E.: Phenology shifts at start vs. end of growing season in temperate vegetation over the Northern Hemisphere for the period 1982–2008, Glob. Change Biol., 17, 2385–2399, doi:10.1111/j.1365-2486.2011.02397.x, 2011.

Krinner, G.: A dynamic global vegetation model for studies of the coupled atmosphere-biosphere system, Global Biogeochem. Cycles, 19, doi:10.1029/2003gb002199, 2005.

Körner, C.: Leaf diffusive conductances in the major vegetation types of the globe, in: Ecophysiology of photosynthesis, edited by: Schulze, E.-D., Springer Verlag, Berlin, 463–490, 1995.

Ladekarl, U.: Soil moisture, evapotranspiration and groundwater recharge in forest and heathland, Ph.D. thesis, Department of earth sciences, University of Aarhus, Denmark, 2001.

Larsen, K. S., Ibrom, A., Jonasson, S., Michelsen, A., and Beier, C.: Significance of cold season respiration and photosynthesis in a subarctic heath ecosystem in Northern Sweden, Glob. Change Biol., 13, 1498–1508, 2007.

Lasslop, G., Reichstein, M., Detto, M., Richardson, A. D., and Baldocchi, D. D.: Comment on Vickers et al.: Self-correlation between assimilation and respiration resulting from flux partitioning of eddy-covariance CO2 fluxes, Agr. Forest Meteorol., 150, 312–314, 2010a.

Lasslop, G., Reichstein, M., Papale, D., Richardson, A., Arneth, A., Barr, A., Stoy, P., and Wohlfahrt, G.: Separation of net ecosystem exchange into assimilation and respiration using a light response curve approach: critical issues and global evaluation, Glob. Change Biol., 16, 187–208, 2010b.

Le Dantec, V., Dufrêne, E., and Saugier, B.: Interannual and spatial variation in maximum leaf area index of temperate deciduous stands, Forest Ecol. Manag., 134, 71–81, 2000.

Leuning, R., Kelliher, F., Pury, D., and Schulze, E.: Leaf nitrogen, photosynthesis, conductance and transpiration: scaling from leaves to canopies, Plant. Cell. Environ., 18, 1183–1200, 1995.

Lloyd, J. and Taylor, J.: On the temperature dependence of soil respiration, Funct. Ecol., 8, 315–323, 1994.

Luo, Y., Wan, S., Hui, D., and Wallace, L.: Acclimatization of soil respiration to warming in a tall grass prairie, Nature, 413, 622–625, 2001.

Luyssaert, S., Inglima, I., Jung, M., Richardson, A., Reichstein, M., Papale, D., Piao, S., Schulze, E., Wingate, L., and Matteucci, G.: CO2 balance of boreal, temperate, and tropical forests derived from a global database, Glob. Change Biol., 13, 2509–2537, 2007.

Mahecha, M. D., Reichstein, M., Carvalhais, N., Lasslop, G., Lange, H., Seneviratne, S. I., Vargas, R., Ammann, C., Arain, M. A., Cescatti, A., Janssens, I. A., Migliavacca, M., Montagnani, L., and Richardson, A. D.: Global Convergence in the Temperature Sensitivity of Respiration at Ecosystem Level, Science, 329, 838–840, doi:10.1126/science.1189587, 2010.

Migliavacca, M., Reichstein, M., Richardson, A. D., Colombo, R., Sutton, M. A., Lasslop, G., Tomelleri, E., Wohlfahrt, G., Carvalhais, N., and Cescatti, A.: Semiempirical modeling of abiotic and biotic factors controlling ecosystem respiration across eddy covariance sites, Glob. Change Biol., 17, 390–409, 2011.

Penuelas, J. and Filella, I.: Phenology feedbacks on climate change, Science, 324, 887–888, doi:10.1126/science.1173004, 2009.

Piao, S., Ciais, P., Friedlingstein, P., Peylin, P., Reichstein, M., Luyssaert, S., Margolis, H., Fang, J., Barr, A., Chen, A., Grelle, A., Hollinger, D. Y., Laurila, T., Lindroth, A., Richardson, A. D., and Vesala, T.: Net carbon dioxide losses of northern ecosystems in response to autumn warming, Nature, 451, 49–52, doi:10.1038/nature06444, 2008.

Pilegaard, K., Hummelshøj, P., Jensen, N., and Chen, Z.: Two years of continuous CO_2 eddy-flux measurements over a Danish beech forest, Agr. Forest Meteorol., 107, 29–41, 2001.

Pilegaard, K., Mikkelsen, T. N., Beier, C., Jensen, N. O., Ambus, P., and Ro-Poulsen, H.: Field measurements of atmosphere-biosphere interactions in a Danish beech forest, Boreal Environ. Res., 8, 315–333, 2003.

Pilegaard, K., Ibrom, A., Courtney, M. S., Hummelshøj, P., and Jensen, N. O.: Increasing net CO_2 uptake by a Danish beech forest during the period from 1996 to 2009, Agr. Forest Meteorol., 151, 934–946, 2011.

Reichstein, M., Papale, D., Valentini, R., Aubinet, M., Bernhofer, C., Knohl, A., Laurila, T., Lindroth, A., Moors, E., Pilegaard, K., and Seufert, G.: Determinants of terrestrial ecosystem carbon balance inferred from European eddy covariance flux sites, Geophys. Res. Lett., 34, L01402, doi:10.1029/2006gl027880, 2007.

Richardson, A. and Hollinger, D.: Statistical modeling of ecosystem respiration using eddy covariance data: maximum likelihood parameter estimation, and Monte Carlo simulation of model and parameter uncertainty, applied to three simple models, Agr. Forest Meteorol., 131, 191–208, 2005.

Richardson, A., Hollinger, D., Aber, J., Ollinger, S., and Braswell, B.: Environmental variation is directly responsible for short but not long term variation in forest atmosphere carbon exchange, Glob. Change Biol., 13, 788–803, 2007.

Richardson, A., Hollinger, D., Dail, D., Lee, J., Munger, J., and O'keefe, J.: Influence of spring phenology on seasonal and annual carbon balance in two contrasting New England forests, Tree Physiol., 29, 321–331, doi:10.1093/treephys/tpn040, 2009.

Richardson, A., Andy Black, T., Ciais, P., Delbart, N., Friedl, M., Gobron, N., Hollinger, D., Kutsch, W., Longdoz, B., and Luyssaert, S.: Influence of spring and autumn phenological transitions on forest ecosystem productivity, Phil. Trans. R. Soc. B, 365, 3227–3246, doi:10.1098/rstb.2010.0102, 2010.

Sage, R. F. and Kubien, D. S.: The temperature response of C3 and C4 photosynthesis, Plant.

Cell. Environ., 30, 1086-1106, doi:10.1111/j.1365-3040.2007.01682.x, 2007.

Siqueira, M., Katul, G., Sampson, D., Stoy, P., Juang, J. Y., McCarthy, H., and Oren, R.: Multi-scale model intercomparisons of CO2 and H2O exchange rates in a maturing southeastern US pine forest, Glob. Change Biol., 12, 1189–1207, 2006.

Sitch, S., Smith, B., Prentice, I. C., Arneth, A., Bondeau, A., Cramer, W., Kaplan, J. O., Levis, S., Lucht, W., and Sykes, M.: Evaluation of ecosystem dynamics, plant geography and terrestrial carbon cycling in the LPJ dynamic global vegetation model, Glob. Change Biol., 9, 161–185, 2003.

Stoy, P. C., Richardson, A. D., Baldocchi, D. D., Katul, G. G., Stanovick, J., Mahecha, M. D., Reichstein, M., Detto, M., Law, B. E., Wohlfahrt, G., Arriga, N., Campos, J., McCaughey, J. H., Montagnani, L., Paw U, K. T., Sevanto, S., and Williams, M.: Biosphere-atmosphere exchange of CO2 in relation to climate: a cross-biome analysis across multiple time scales, Biogeosciences, 6, 2297–2312, doi:10.5194/bg-6-2297-2009, 2009.

Tanja, S., Berninger, F., Vesala, T., Markkanen, T., Hari, P., Mäkelä, A., Ilvesniemi, H., Hänninen, H., Nikinmaa, E., and Huttula, T.: Air temperature triggers the recovery of evergreen boreal forest photosynthesis in spring, Glob. Change Biol., 9, 1410–1426, 2003.

Teklemariam, T., Lafleur, P., Moore, T., Roulet, N., and Humphreys, E.: The direct and indirect effects of Interannual meteorological variability on ecosystem carbon dioxide exchange at a temperate ombrotrophic bog, Agr. Forest Meteorol., 150, 1402–1411, 2010.

Thum, T., Aalto, T., Laurila, T., Aurela, M., Lindroth, A., and Vesala, T.: Assessing seasonality of biochemical CO2 exchange model parameters from micrometeorological flux observations at boreal coniferous forest, Biogeosciences, 5, 1625–1639, doi:10.5194/bg-5-1625-2008, 2008.

Valentini, R., Matteucci, G., Dolman, A., Schulze, E. D., Rebmann, C., Moors, E., Granier, A., Gross, P., Jensen, N., and Pilegaard, K.: Respiration as the main determinant of carbon balance in European forests, Nature, 404, 861–865, 2000.

Vesala, T., Launiainen, S., Kolari, P., Pumpanen, J., Sevanto, S., Hari, P., Nikinmaa, E., Kaski, P., Mannila, H., Ukkonen, E., Piao, S. L., and Ciais, P.: Autumn temperature and carbon balance of a boreal Scots pine forest in Southern Finland, Biogeosciences, 7, 163–176, doi:10.5194/bg-7-163-2010, 2010.

Vickers, D., Thomas, C. K., Martin, J. G., and Law, B.: Self-correlation between assimilation and respiration resulting from flux partitioning of eddy-covariance CO2 fluxes, Agr. Forest Meteorol., 149, 1552–1555, 2009.

Wang, Y. P., Baldocchi, D., Leuning, R. A. Y., Falge, E. V. A., and Vesala, T.: Estimating parameters in a land-surface model by applying nonlinear inversion to eddy covariance flux measurements from eight FLUXNET sites, Glob. Change Biol., 13, 652–670, doi:10.1111/j.1365-2486.2006.01225.x, 2007.

Yuan, W., Luo, Y., Richardson, A., Oren, R., Luyssaert, S., Janssens, I., Ceulemans, R., Zhou, X., Grünwald, T., and Aubinet, M.: Latitudinal patterns of magnitude and interannual variability in net ecosystem exchange regulated by biological and environmental variables, Glob. Change Biol., 15, 2905–2920, 2009.

Zhou, X., Weng, E., and Luo, Y.: Modeling patterns of nonlinearity in ecosystem responses to temperature, CO2, and precipitation changes, Ecol. Appl., 18, 453–466, 2008.

Table 1. Mean annual climate variables, gap-filled and modelled NEE and model error statistics for the modified hyperbolic light response model of forest-atmosphere CO_2 exchange (Eq. 3).

Year	Mean annual climate			Gap-filled NEE and model predictions		Statistics of the model errors			
	T_{air}	R_g	SWC	NEE_{obs}	NEE_{model}	N	r^2	RMSE	MAE
1997	8.3	118	23	−56	−89	13 824	0.79	2.89	0.02
1998	7.8	103	27	32	55	15 367	0.86	2.81	0.04
1999	8.7	108	27	−78	−28	14 955	0.77	3.68	0.13
2000	8.8	104	24	−113	−115	15 361	0.84	3.23	0.07
2001	7.9	109	26	−158	−197	16 110	0.85	3.08	0.09
2002	8.7	114	26	−157	−198	15 764	0.86	2.66	0.1
2003	8.3	121	21	−116	−205	12 848	0.84	3.38	0.1
2004	8.0	110	24	−165	−331	12 611	0.81	3.97	0.08
2005	8.2	113	22	−209	−299	13 075	0.85	3.01	0.17
2006	9.0	109	23	−119	−72	15 675	0.82	3.38	0.1
2007	9.3	116	NA	−229	−344	14 910	0.85	3.24	0.19
2008	9.2	126	NA	−344	−392	16 155	0.85	3.17	0.13
2009	8.6	125	21	−331	−368	16 523	0.85	3.22	0.08
Mean	8.5	114	21	−157	−199	14 860	0.83	3.21	0.08

Air temperature, T_{air} (°C) and global radiation, R_g ($W\,m^{-2}$) were measured above canopy. Soil water content, SWC (%) was measured at 0–10 cm, the system broke down temporarily in 2007–2008. Methods for the gap-filling of the observed NEE, NEE_{obs} ($g\,C\,m^{-2}\,yr^{-1}$) and modelled NEE, NEE_{model} ($g\,C\,m^{-2}\,yr^{-1}$) are described in the text. Model error statistics include, the number of valid observation (N) used for parameter estimation in each year, coefficient of determination (r^2), root mean squared error (RMSE) and mean absolute error (MAE).

Table 2. Bivariate correlation coefficients between annual anomalies in NEE, GPP and TER and mean annual climate variables including air temperature (T_{air}), global radiation (R_g), soil water content (SWC) and precipitation (PPT).

	NEE	GPP	TER	T_{air}	R_g	SWC	PPT
NEE	1	−0.7 (**)	0.09	−0.49	−0.73 (**)	0.62 (*)	0.08
GPP	−0.7 (**)	1	0.65 (*)	0.34	0.24	0.34	0.07
TER	0.09	0.65 (*)	1	−0.06	−0.44	0.14	0.19
T_{air}	−0.49	0.34	−0.06	1	0.35	−0.15	0.33
R_g	−0.73 (**)	0.24	−0.44	0.35	1	−0.77 (**)	−0.3
SWC	0.62 (*)	0.34	0.14	−0.15	−0.77 (**)	1	0.76 (**)
PPT	0.08	0.07	0.19	0.33	−0.3	0.76 (**)	1

Statistically significant correlations are marked with ** ($p < 0.01$) and * ($p < 0.05$).

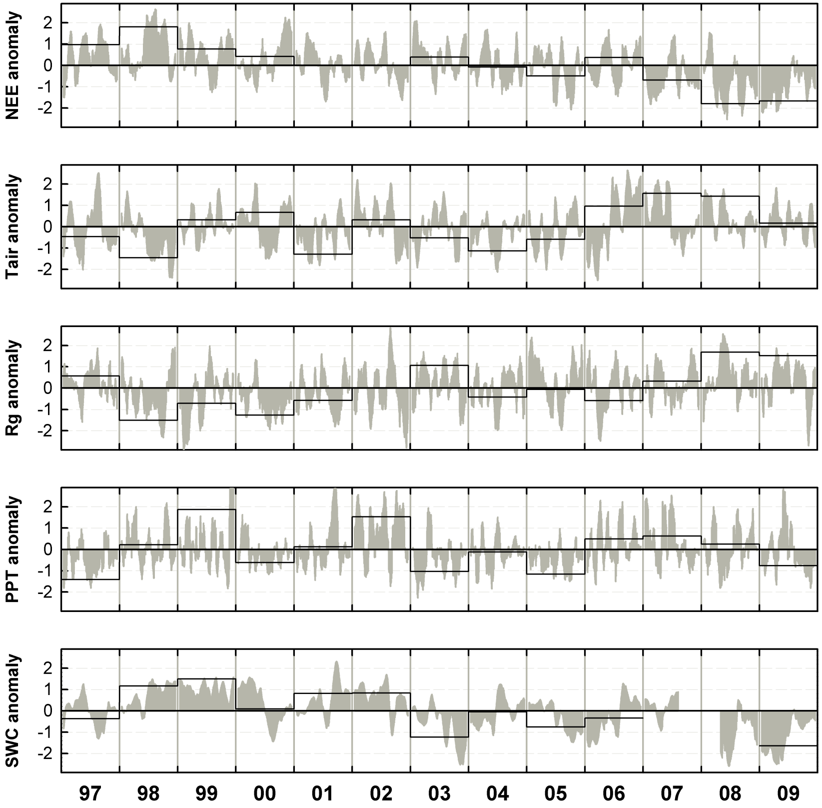

Fig. 1. Deviation of NEE, air temperature (T_{air}), global radiation (R_{g}), precipitation (PPT) and soil water content (SWC) from the 13-year annual average (wide black bar) and daily average values (grey areas). The daily data was smoothed with a 30 day moving average. The y-axis gives the standard deviation from the mean (e.g. the annual NEE anomaly in 1998 is about 2 SD above the 13-year average with less uptake of carbon).

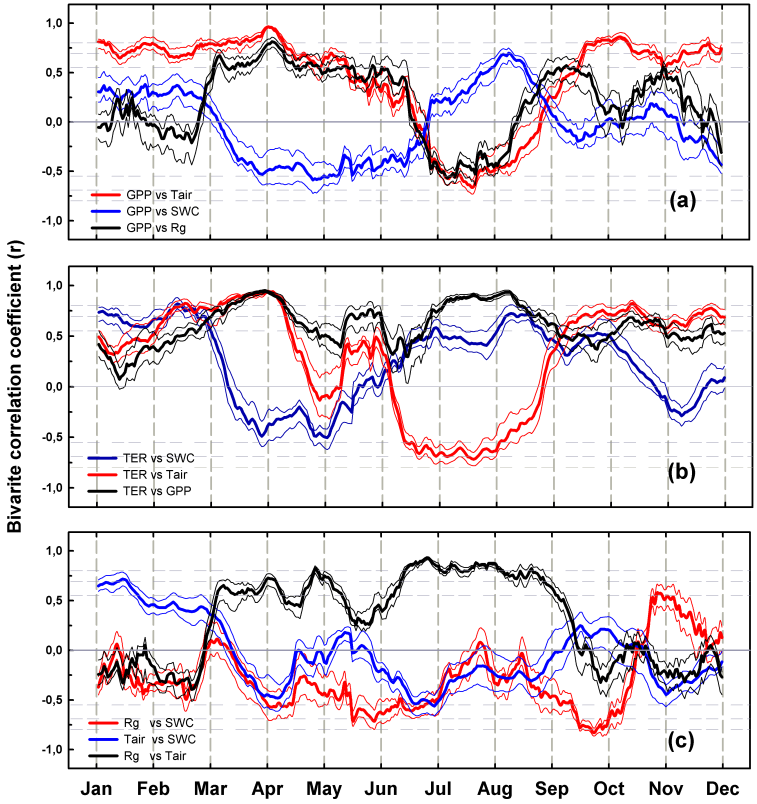

Fig. 2. Bivariate correlation between: **(a)** periodical GPP integral (30 day moving window) with periodical mean air temperature (T_{air}), soil water content (SWC) and global radiation (R_g). **(b)**: periodical TER integral with periodical mean climate variables and GPP. **(c)**: the climate variables. Dashed horizontal lines indicate different levels of statistical significance ($P = 0.05$, 0.01 and 0.001). The envelope of the bold line indicates the uncertainties (95 percentile) of the correlation coefficients, as data of each individual year was excluded from the correlation analysis.

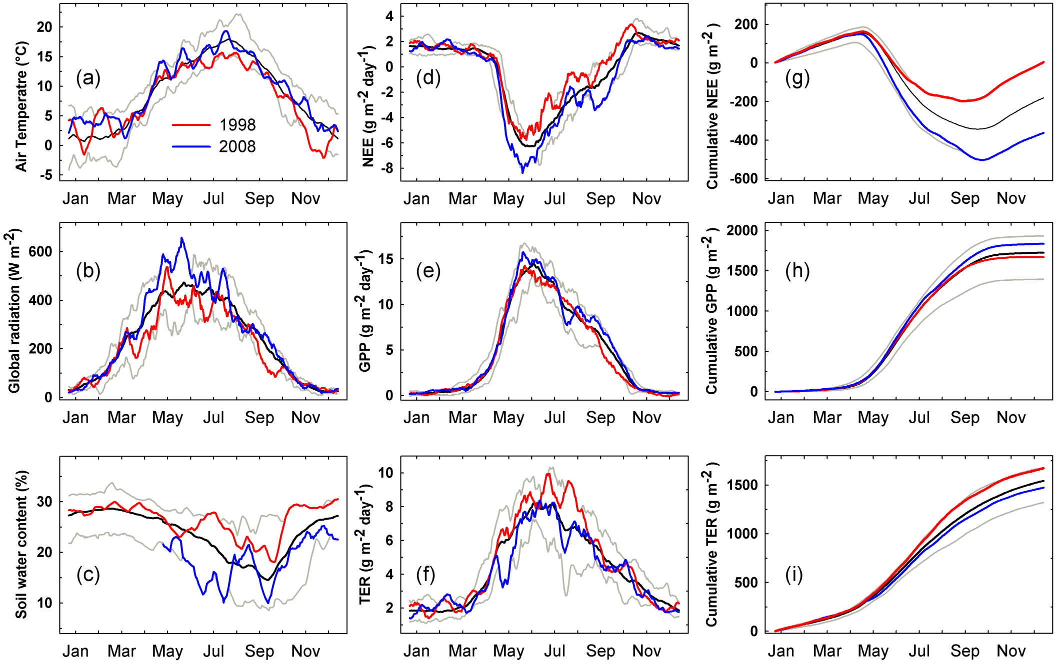

Fig. 3. The average (black line) and example years (1998, 2008) in terms of climate **(a, b, c)**, carbon flux **(d, e, f)** and cumulative carbon flux **(g, h, i)**. All data were smoothed with a 14-day moving average. Grey lines indicate the maximum and minimum of the value on the same DOY across the 13 years.

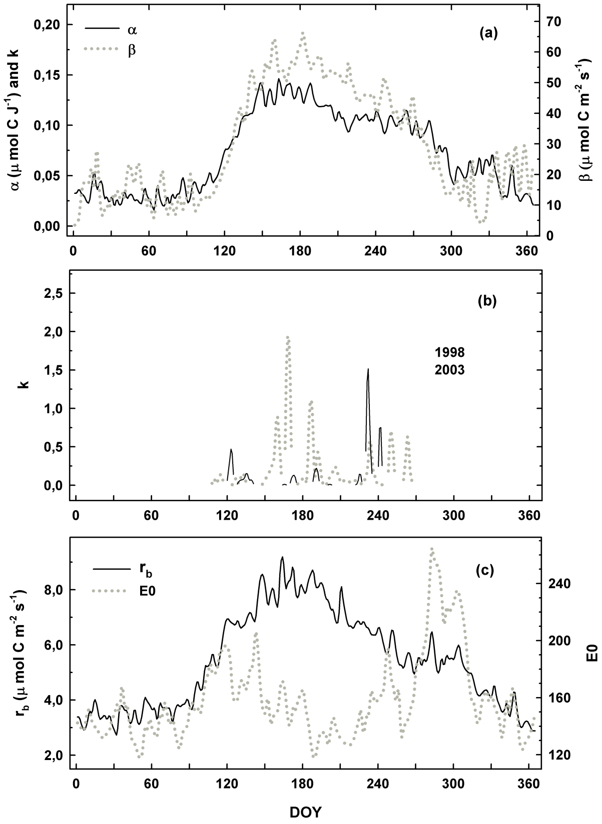

Fig. 4. **(a)** Seasonal variation in: light use efficiency, α; maximum photosynthetic capacity, β; **(b)** Seasonal variation in k, the scaling parameter of VPD limitation on β. **(c)** Seasonal variation in: base respiration r_b and temperature sensitivity of the respiration, E_0. The parameter time series were presented as an ensemble (mean value) of all the 13 years, except for the k, where the values in 1998 and 2003 were presented as examples.

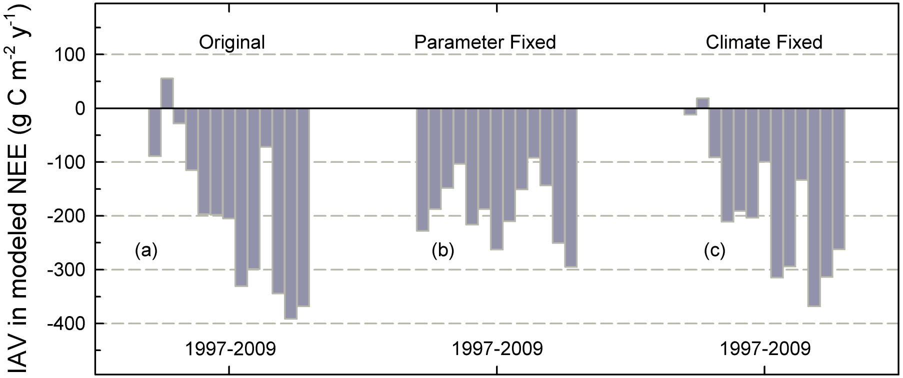

Fig. 5. Interannual variation in modelled NEE **(a)** F_{original}: using the original climate and parameter time series in each of the 13 years; **(b)** F_{parfixed}: parameters kept constant; **(c)** F_{clifixed}: climate kept constant. Each value of F_{parfixed} and F_{clifixed} represents an ensemble mean value of the 13 simulations where the parameter, or climate time series from 1997–2009 was applied in sequence.

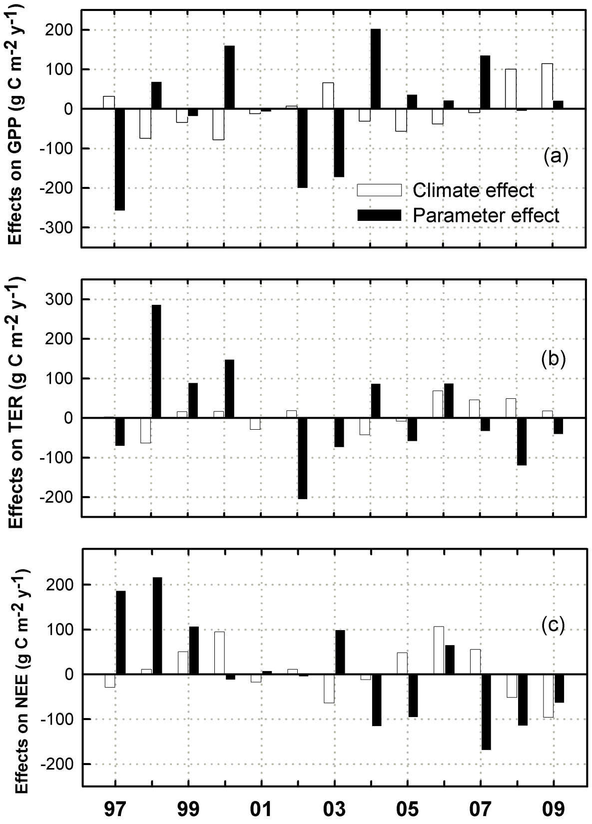

Fig. 6. Effects attributed to climate and parameter on the interannual variation on modelled GPP, TER and NEE. The values are determined as the difference between the mean of the original modelled fluxes and those calculated with an ensemble mean value of simulation where the parameter, or climate time series from 1997–2009 was applied in sequence (F_{parfixed} and F_{clifixed}; cf. Fig. 5 for NEE).

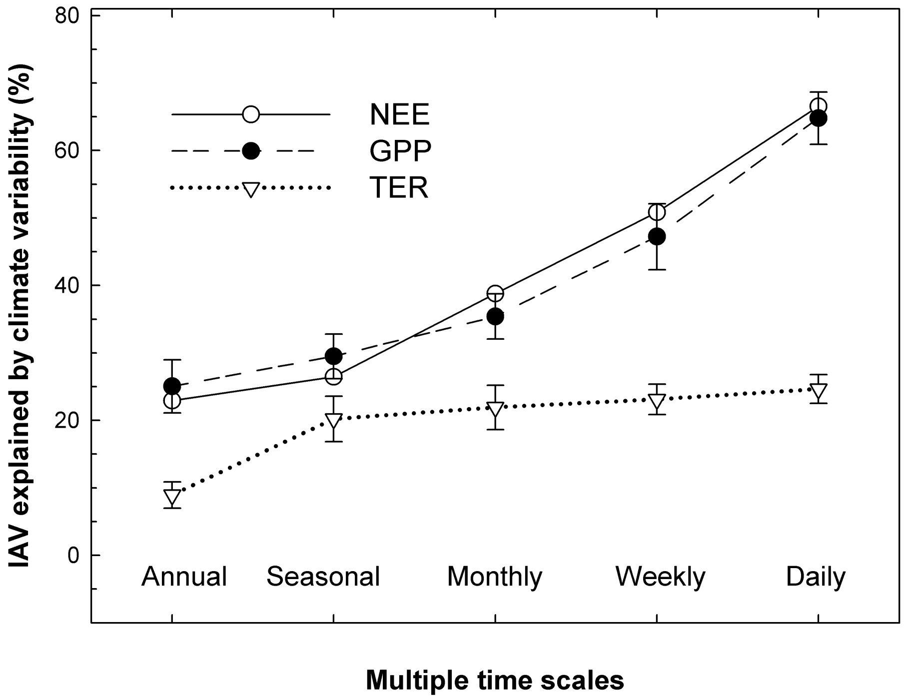

Fig. 7. Percentage of interannual variation in modelled carbon fluxes caused by climate variability at different time scales. The error bar represents the standard deviation of the estimates (cf. Eq. 6).

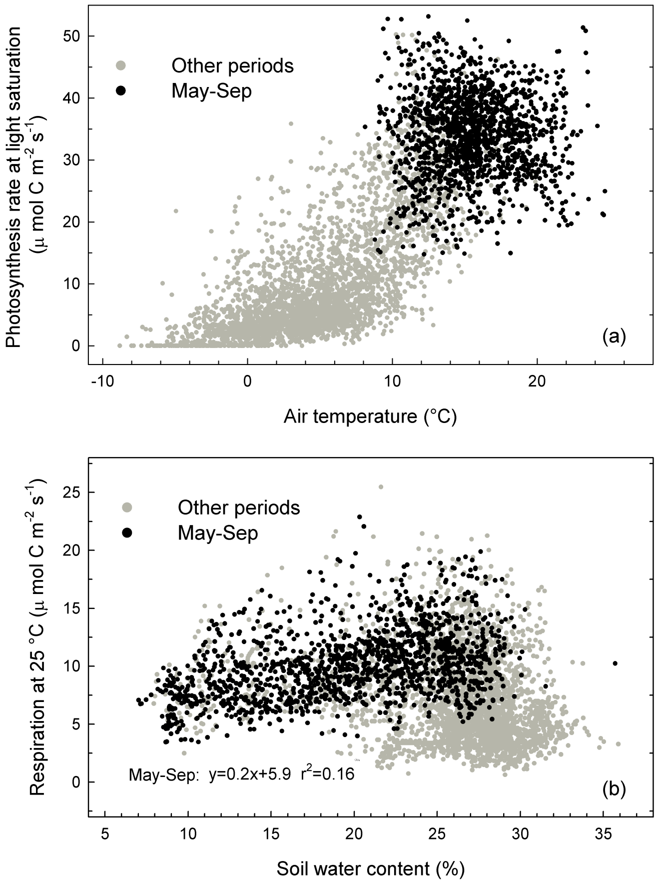

Fig. 8. Possible covariance between climate and estimated parameters. **(a)** GPP at light saturation affected by air temperature. **(b)** TER at 25 °C affected by soil water content.