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TELLUS

Biophysical controls on CO_2 fluxes of three Northern forests based on long-term eddy covariance data

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ABSTRACT

Six to nine years of net ecosystem carbon exchange (NEE) data from forests in Hyytiälä in Finland, Sorø in Denmark and Norunda in Sweden were used to evaluate the interannual variation in the carbon balance. For half-monthly periods, average NEE was calculated for the night-time data. For the daytime data parameters were extracted for the relationship to photosynthetic active radiation (PAR). The standard deviation of the parameters was highest for Norunda where it typically was around 25% of the mean, while it was ca. 15% for Hyytiälä and Sorø. Temperature was the main controller of respiration and photosynthetic capacity in autumn, winter and spring but explained very little of the interannual variation in summer. A strong correlation between respiration and photosynthesis was also revealed. The start, end and length of the growing season were estimated by four different criteria. The start date could explain some of the variation in yearly total NEE and gross primary productivity (GPP) in Hyytiälä and Sorø, but the average maximum photosynthetic capacity in summer explained more of the variation in annual GPP for all sites than start, end or length of the growing season.

1. Introduction

From a climate change perspective, the most important term in the carbon balance of vegetation is the *net* ecosystem exchange (NEE), that is, the difference between two large fluxes, the total ecosystem respiration and the gross primary productivity (GPP). The fact that NEE is the result of the imbalance of two large fluxes makes it sensitive to small relative changes in these terms (e.g. Lindroth et al., 1998). After more than a decade of intense studies of the carbon balance of vegetation, we are still not able to explain very well the large interannual variability of the NEE. The reason for this could be that so many factors, biological as well as physiochemical, affect the processes behind the fluxes and since many processes are linked to each other, the system becomes very complex.

The processes of photosynthesis are well known (Farquhar et al., 1980, 2001) and can be successfully modelled (e.g. Baldocchi and Harley, 1995). In cold climates the most difficult part is probably the description of the decline of the photosynthetic capacity in the autumn and the recovery after the dormancy period in the winter (Lundmark et al., 1998; Randersson et al., 1999).

To fully understand and model the processes of respiration is a more challenging issue than to understand the photosynthesis but a great deal of research has been done and understanding is increasing (e.g. Reichstein et al., 2003; Davidson and Janssens, 2006). The total ecosystem respiration is a complex process that is made up of autotrophic and heterotrophic respiration, and is controlled by factors such as air and soil temperature, soil water content, activity of the plant and the quality of the soil organic matter (e.g. Ågren et al., 1980; Orchard and Cook, 1983; Lloyd and Taylor, 1994; Ceschia, 2001). There is also a strong link between photosynthesis and respiration as the respiration is dependent on the sources of carbon that are produced by the photosynthesis (Ryan and Law, 2005).

Long-term studies of net ecosystem exchange started in the middle of the 1990's along with the introduction of the eddy covariance methodology (Aubinet et al., 2000). Today there are

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several sites that can show more or less continuous records over more than 5 yr (http://www-eosdis.ornl.gov/FLUXNET/). To better understand the processes behind the measured NEE, the flux is commonly divided into total respiration and photosynthesis by extrapolation of the night-time data by using relationships to temperature (Falge et al., 2002). Analysis of measurements over several years will hopefully give insight into which factors determine NEE. However, the great number of physical, biological and anthropogenic factors, such as management and air pollution, that may have important effects to the carbon balance and the difficulties of setting up large-scale controlled experiments make the task hard.

The aim of this study is to quantify and explain the interannual variation in the seasonal course of photosynthesis and ecosystem respiration for three forests in Northern Europe. The evaluation is based on estimation of parameters of a light response function during daytime and on mean respiration rates during the night for half-monthly periods. These parameters' relationships to environmental variables were then analysed.

2. Materials and method

2.1. Site description

The sites included in the study are Hyytiälä in southern Finland (61°50′51″N, 24°17′42″E, 181 m alt), Sorø in eastern Denmark (55°29′13″N, 11°38′45″E, 40 m alt) and Norunda in central Sweden (60°05′10″N, 17°29′56″E, 45 m alt).

The Hyytiälä forest is a homogeneous Scots pine stand (*Pinus sylvestris* L.) planted in 1962 and it grows on a Haplic podzol. The ground vegetation is dominated by dwarf shrubs (*Calluna vulgaris* L., *Vaccinium vitis-idaea* L. and *V. myrtillus* L.) and mosses. An area of 4.33 ha was thinned between January and March 2002. In 2005, the average tree height was 13.9 m and the projected leaf area per ground area unit (LAI) was 2.5. LAI for Hyytiälä was calculated from a measured total leaf area index of 6.5 divided by 2.6. The mean annual temperature in 1961–1990 was +2.9 °C and the annual sum of precipitation 709 mm.

The forest in Sorø consists mainly of beech (*Fagus sylvatica* L.) that grows on a Mollisol. There are also some small stands (mainly Norway spruce [*Picea abies* (L.) Karst.)] and single trees (e.g. European larch (Larix deciduas Mill.)) of conifers that occupy in total ca. 20% of the footprint area. In the early spring there is a flush of mainly *Mercurialis perennis* L. and *Anemone nemorosa* L. on the forest floor but after bud break of the trees there is only some sparse grass vegetation. In 2002 the trees were 82 years old, had reached an average height of 25 m and had a peak seasonal LAI of about 5. The mean annual temperature was +8.3 °C and the annual sum of precipitation 730 mm.

In Norunda the forest was naturally regenerated at the end of the 19th century on a Dystric Regosol. Of the basal area 65% is Scots pine, 33% is Norway spruce and the rest is deciduous trees. The ground vegetation is dominated by dwarf shrubs (*Vaccinium myrtillus* L. and *V. vitis-idaea* L.), grasses and mosses. The LAI is 4–5 and the dominant height is 27.8 m. The mean annual temperature in 1961–1990 was +5.5 °C and the annual sum of precipitation 527 mm.

2.2. Measurements

The net ecosystem exchange (NEE) was measured at all sites by the eddy covariance technique following the Euroflux methodology (Aubinet et al., 2000). There is basically the same system at all sites consisting of a Gill ultrasonic anemometer (R2 or R3; Solent, Lymington, UK) and an infrared closed-path gas analyser (Li-6262; Li-Cor Inc, Lincoln, USA) mounted on a tower above the tree canopy. Markkanen et al. (2001), Pilegaard et al. (2003) and Grelle et al. (1999) describe the details of the measurements in Hyytiälä, Sorø and Norunda, respectively.

Environmental variables were measured in the same towers as the fluxes except soil water content (SWC) that was measured in the surroundings, and the radiation measurements in Hyytiälä that were taken on a separate tower 30 m from the main tower. The variables that were used in this study were air temperature above the canopy, relative humidity, photosynthetic active radiation (PAR) and SWC. Specification of the instrumentation can be found in Markkanen et al. (2001), Pilegaard et al. (2003) and Lundin et al. (1999) for Hyytiälä, Sorø and Norunda, respectively.

Data used in this study were from January 2000 to June 2006 for Hyytiälä, January 2000 to December 2005 for Sorø and January 1995 to October 2003 for Norunda.

2.3. Data analysis

Quality checked data were first filtered by a friction velocity threshold of 0.30 m s^{-1} for Sorø and Norunda and 0.25 m s^{-1} for Hyytiälä to make sure that the fluxes were from well-mixed conditions. The 30-min data were then split to daytime and night-time by a PAR threshold of 10 μmol m^{-2} s^{-1}. For the night-time data, averages of NEE, air temperature and SWC were calculated for half-monthly periods. For the daytime data, averages of air temperature, PAR and vapour pressure deficit (VPD) were calculated for the same periods. A light response function (Falge et al., 2001) was fitted to the daytime NEE (F_c, μmol m^{-2} s^{-1}, negative values means that the ecosystem takes up carbon) for the half-monthly periods.

$$F_c = -(F_{c\,sat} + R_d)\left[1 - \exp\left(\frac{-\alpha Q}{F_{c\,sat} + R_d}\right)\right] + R_d \qquad (1)$$

where saturation flux (F_{csat}, μmol m^{-2} s^{-1}), dark respiration (R_d, μmol m^{-2} s^{-1}) and quantum efficiency (α, mol mol^{-1}) are fitted parameters and Q is PAR (μmol m^{-2} s^{-1}). As a value of the maximum gross primary productivity (GPP_{max}) the function value with $Q = 2000$ μmol m^{-2} s^{-1}, without the last R_d term and given a positive sign, was used.

2.4. Growing season length

The start and end of the growing season was determined using three different approaches. In the first method a simple threshold of 4.7 °C averaged weekly air temperature was used; this was the common value of a five day running average air temperature that was best related to growing season length for some evergreen boreal sites (Suni et al., 2003b). As another potential method to identify the start and end of the growing season, the average night-time ($Q < 10$ μmol m^{-2} s^{-1}) and noon (10:00–14:00) NEE was calculated for 1-week periods. Based on the long-term maximum difference between night and noon NEE, the growing season was defined as the period when the difference was more than 5 or 10% of the maximum difference occurring during the growing season. In the last approach a rough estimate of the net primary production (NPP) was calculated, as it is reasonable that NPP is positive during the growing season:

$$\mathrm{NPP} = 4 \times 3600(\mathrm{NEE_{night}} - \mathrm{NEE_{noon}})/f_{\mathrm{Q}} - 24 \times \times 3600\mathrm{NEE_{night}}/f_{\mathrm{R}}. \quad (2)$$

Daily total NPP (μmol m^{-2}) was calculated from average $\mathrm{NEE_{night}}$ and $\mathrm{NEE_{noon}}$ (μmol m^{-2} s^{-1}). To scale the 4-h noon period to total daily GPP the fraction of the daily total PAR between 10:00 and 14:00 (f_{Q}) was used. f_{R} is the autotrophic fraction of the total ecosystem respiration. It is difficult to measure f_{R} and there were no data available for any of the sites. For Hyytiälä and Sorø a value of 0.65 was taken as an average value from a modelling study in Sweden (Lagergren et al., 2006) where Biome-BGC (Thornton, 1998) was used. Norunda has been shown to have unusually high heterotrophic respiration in several studies (e.g. Valentini et al., 2000; Widén and Majdi, 2001) and therefore a value of 0.55 was assumed for this site. This simple model of NPP assumes that the ecosystem respiration is equal at day and night, that GPP is linearly related to PAR and that f_{R} is constant over the season. These are all rough assumptions, but since the only point of interest is whether NPP is positive or negative it should not be too crucial. For all approaches, the start was determined as the first week after which the criterion was constantly higher than the limit and the end when it was persistently below it.

The start, end and length of the growing season was compared to yearly total NEE and GPP. At all sites the basic principle for calculation of GPP was the same; the total ecosystem (R_{eco}) respiration was modelled from night-time data of NEE fitted to a type of exponential function by temperature, and GPP was calculated as the difference between NEE and R_{eco} (Falge et al., 2002). For Hyytiälä the methodology followed Mäkelä et al. (2006), in Sorø R_{eco} was modelled for monthly periods and gap filling was based on running averages and in Norunda R_{eco} was modelled for running 2-week periods and gap filling was based on a light-response function. Different gap filling techniques can result in biased conclusions when comparing different sites but in this study there were no comparisons of absolute values between sites and we therefore used the method each principal investigator considered as most useful. For all analysis except yearly total NEE and GPP non-gap-filled data were used. The data coverage is given in Table 1.

3. Results and discussion

3.1. Light response parameters

The mean seasonal course of the light response parameters F_{csat} and α showed a similar pattern for the coniferous forests in

Table 1. Yearly total NEE and GPP (g C m^{-2} yr^{-1}), with mean and standard deviation, for the three sites.

Hyytiälä	2000	2001	2002	2003	2004	2005	Mean	*SD*
NEE	−189	−179	−232	−136	−226	−230	−199	38
GPP	1094	991	1084	974	1068	1070	1047	51
Gap filled	38.6	34.7	37.4	35.1	34.9	44.9		
Sorø	2000	2001	2002	2003	2004	2005	Mean	*SD*
NEE	−161	−196	−233	−289	−157	−141	−196	56
GPP	1540	1589	1456	1549	1785	1750	1612	129
Gap filled	42.3	37.1	38.0	49.0	55.0	45.7		

Norunda	1995	1996	1997	1998	1999	2000	2001	2002	Mean	*SD*
NEE	105	−1	77	67	0	105	80	−15	52	50
GPP	1089	1142	1056	1129	1048	1020	1011	1102	1075	49
Gap filled	30.9	36.6	33.2	37.1	33.2	36.1	51.8	56.1		

The fraction of data rejected because of the friction velocity criterion or missing for other reasons such as system maintenance or malfunctioning is also given (gap filled, %).

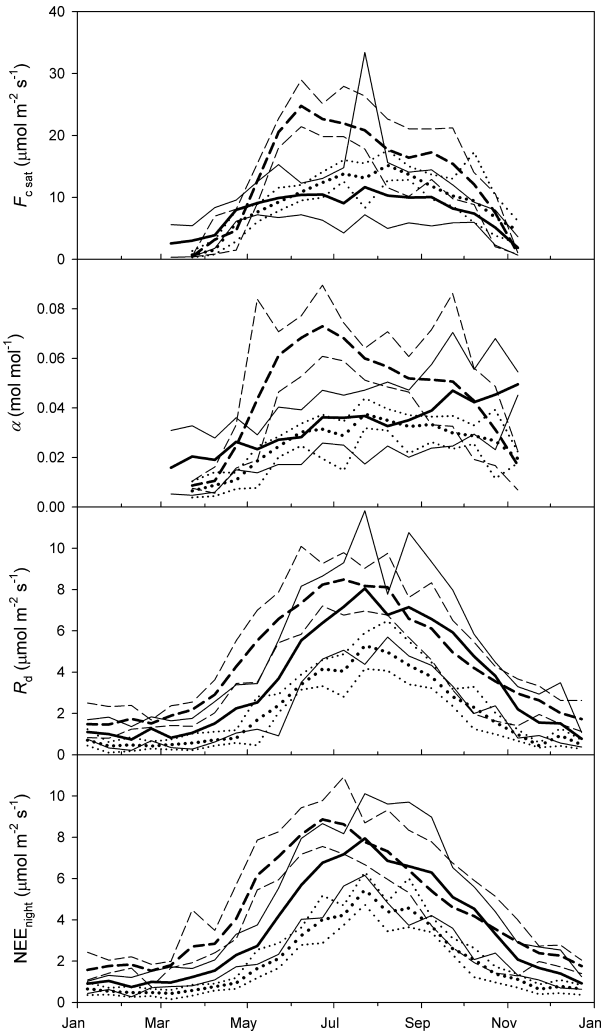

Fig. 1. The seasonal course of the average (thick lines), minimum and maximum (thin lines) half-monthly values of the parameters describing daytime NEE (see eq. 1) and night-time NEE for Hyytiälä (dotted lines), Sorø (dashed lines) and Norunda (solid lines).

Hyytiälä and Norunda (Fig. 1). For Sorø F_{csat} reached its highest value in the first half of June and after that it slowly decreased until October when leaf senescence started. The pattern was similar for α but the variation was larger, especially in the spring. In Hyytiälä and Norunda F_{csat} varied over the season in close relationship with air temperature. For Norunda α increased linearly from March to the beginning of November. The maximum and minimum values of the parameters deviated by ±10–30% from the long-term mean. The deviation was highest for Norunda where the standard deviation was typically around 25% of the mean while it was ca. 15% for Hyytiälä and Sorø. In Sorø the variation in F_{csat} was twice as high at the end of the summer compared to the beginning. In the second half of July in 1996 an extremely high value of F_{csat} was achieved in Norunda and at the same time α was lower than normal, which means that the light response showed low sensitivity and had no distinct light saturation level (eq. 1). An extra check of the data did not reveal any problems with the data or measurements and it was decided to keep the value.

The absolute values of the light-response parameters are in the top or in the middle of the range found in a wider study of Northern Europe forests (Lindroth et al., 2007). In Hyytiälä no clear effect of the thinning in early 2002 (data not shown) on the parameter values could be seen and it was also concluded in a previous study that the thinning had very little impact on the water and carbon fluxes (Vesala et al., 2005).

3.2. *Respiration*

The night-time NEE and R_d showed very similar dynamics, which were tightly related to the temperature (Fig. 1), and for respective sites, the absolute values of night NEE and R_d were close. The deviation from the mean was in relative terms lowest in the summer for all three sites. Sorø and Norunda had about the same respiration in the middle of the summer and autumn but Sorø hade higher rates in the winter and spring. Hyytiälä's maximum rate reached ca. 65% of the other sites but in winter was only ca. 30% of the Sorø values. The absolute values of night time NEE and R_d are within the range reported as minimum and maximum seasonal 15-d mean values derived from extrapolation of night-time fluxes for a large number of forests (Falge et al., 2002).

3.3. *Relationships to environmental variables*

To analyse the dependency of the interannual variation in the half-monthly values of respiration and GPP_{max} on environmental variables, linear relationships were fitted for 1-month periods. At the beginning and end of the growing season GPP_{max} was positively related to temperature at all sites but in summer there was no relationship or a negative one (Fig. 2). A negative relationship between SWC and GPP_{max}, as can be seen in the beginning of the growing season in Hyytiälä and Sorø, is not reasonable but an explanation could be that SWC covaries with some other variable. From July to September the relationship was positive at all sites and SWC accounts for up to 50% of the between year variation of GPP_{max}.

Temperature is generally considered as a major factor controlling respiration (e.g. Lloyd and Taylor, 1994) and in autumn, winter and spring it explains more than 40% of the interannual variation in night-time NEE except for January–March in Norunda (Fig. 3). The weaker correlation for the first months of the year in Norunda could be explained by the fact that the snow cover varies a lot between different years at this site, which has implication for how strongly soil respiration is connected to air temperature. By contrast, night-time temperature

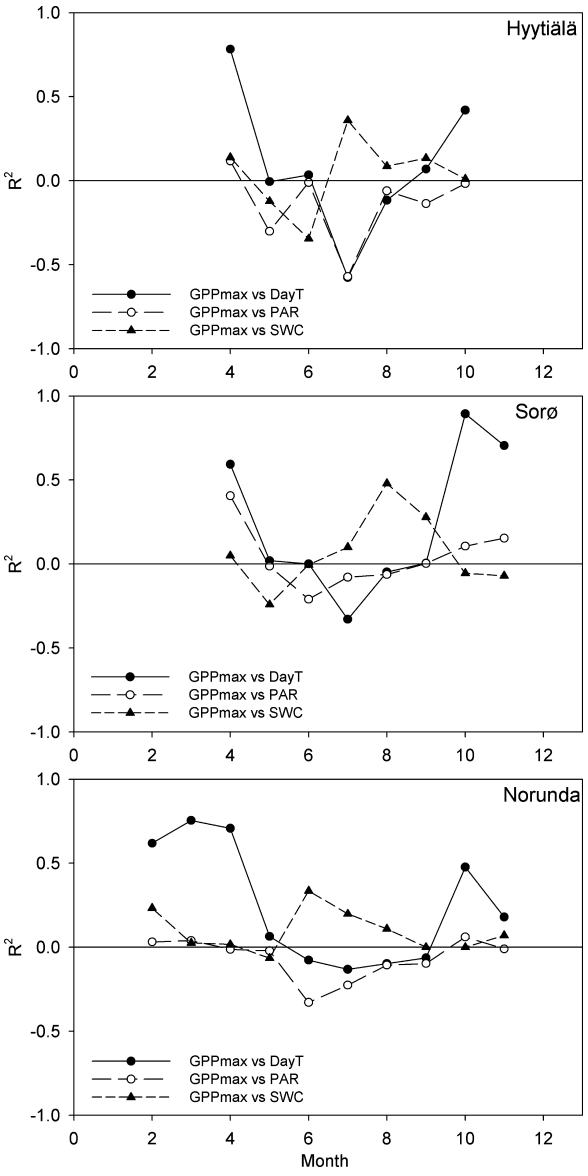

Fig. 2. R^2 values for linear regressions fitted to 1-month periods between half-monthly derived values of maximum photosynthetic capacity (GPP_{max}) and environmental variables. GPP_{max} was calculated from the light response functions (see eq. 1) for 2000 μmol m^{-2} s^{-1} of PAR.

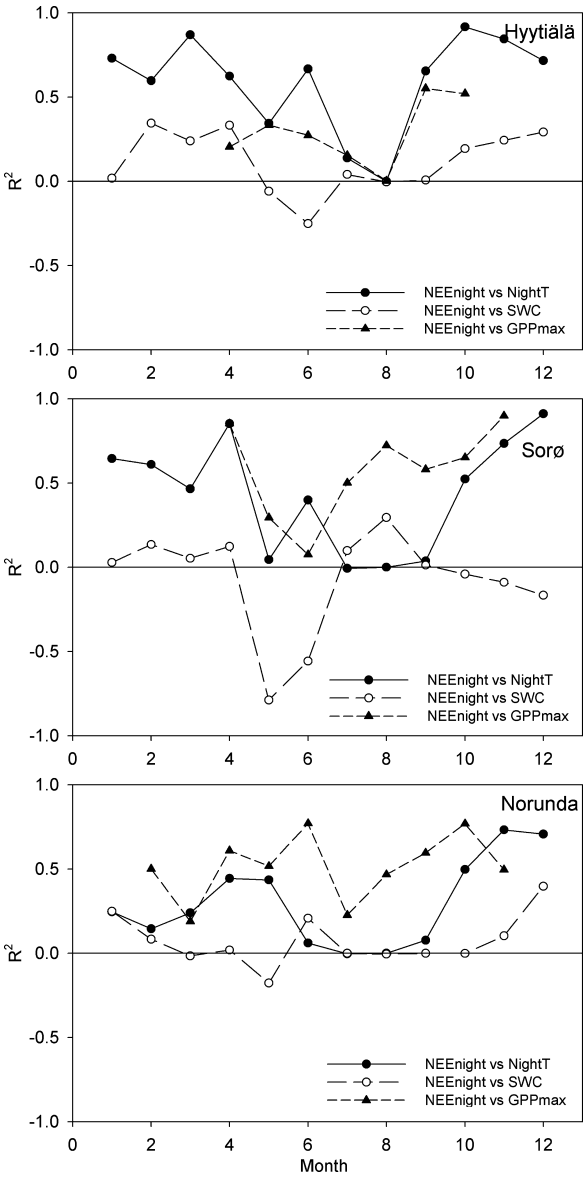

Fig. 3. R^2 values for linear regressions fitted to 1-month periods between half-monthly derived values of night-time average NEE (NEE_{night}) and environmental variables.

explained less than 15% of the between year variation in night-time NEE for July and August in Hyytiälä, May–September (with the exception of June) in Sorø and June–September in Norunda (Fig. 3). Instead there is mostly a much stronger relationship between respiration and GPP_{max}, which is in line with recent research (Janssens et al., 2001; Ryan and Law, 2005). The reason for weaker relationships for Hyytiälä could be that there is a lag between respiration and production that could be longer further north.

The interannual variation in the night-time NEE against exponential temperature relationships was tested for full years (Table 2). The variation in Hyytiälä was about half that in Norunda and Sorø but the exponent of the exponential fits was almost the same for all sites. In Norunda, there was less variation in modelled respiration at the mean temperature of the current year than at the long term annual mean temperature, relative *SD* 6.4% (data not shown) compared to 11.6%, which supports that temperature does not regulate the between year variation in respiration. It should, however be mentioned that this analysis is not totally independent from that in Fig. 3.

Table 2. The fits of the night-time NEE (μ mol m^{-2} s^{-1}) to night temperature for the half-monthly averages on the form $NEE_{night} = aEXP(bT_{night})$.

Hyytiälä	2000	2001	2002	2003	2004	2005	Mean	*SD*	*SD*/mean
a	0.914	0.876	0.922	0.879	0.866	0.785	0.874	0.049	5.6%
b	0.108	0.122	0.105	0.116	0.121	0.124	0.116	0.008	6.8%
R^2	0.90	0.96	0.95	0.94	0.94	0.97	0.94		
At 2.9 °C	1.25	1.25	1.25	1.23	1.23	1.12	1.22	0.05	4.0%
Sorø	2000	2001	2002	2003	2004	2005	Mean	*SD*	*SD*/mean
a	1.400	1.737	1.412	1.577	1.656	1.892	1.612	0.191	11.8%
b	0.121	0.100	0.097	0.109	0.122	0.099	0.108	0.011	10.4%
R^2	0.82	0.88	0.73	0.86	0.89	0.84	0.84		
At 8.3 °C	3.83	3.99	3.16	3.88	4.56	4.31	3.96	0.48	12.0%

Norunda	1995	1996	1997	1998	1999	2000	2001	2002	Mean	*SD*	*SD*/mean
a	1.511	1.674	1.459	1.515	1.511	1.144	1.411	1.393	1.452	0.151	10.4%
b	0.117	0.118	0.118	0.130	0.106	0.140	0.106	0.088	0.115	0.016	13.7%
R^2	0.88	0.91	0.78	0.91	0.95	0.92	0.92	0.88	0.89		
At 5.5 °C	2.88	3.20	2.80	3.09	2.70	2.47	2.53	2.26	2.74	0.32	11.6%

The function value at each site's mean annual temperature is also presented.

Depletion of the soil water is a process that can reduce the soil respiration (Orchard and Cook, 1983; Borken et al., 2006). In Sorø, and to some degree also in Hyytiälä, there is however a strong negative relationship between night NEE and SWC in May and June (Fig. 3). The reason for such a pattern could be that a warm and wet winter and spring could be favourable for decomposition and then there are smaller amounts of easily decomposed material in May and June.

3.4. *Growing season length*

Figure 4 shows the average flux for the night and noon periods for the three sites. The magnitude of the two fluxes started to deviate around weeks 12–15 and became similar again around weeks 42–45. However the start and end of the growing season was not always clearly distinguishable, especially in Norunda, and the same applied for the start of the growing season in Sorø. In Norunda and Sorø there was also noticeably higher night than noon NEE for almost all winter months, indicating that there is a small carbon uptake also in winter, which in Sorø most likely is driven by the 20% fraction of conifers.

In Hyytiälä and Norunda the >4.7 °C threshold gave a later start to the season than the other limits (Fig. 5). In Sorø, where respiration in spring is relatively high, the NPP threshold gave a later start to the growing season. In Norunda the temperature limit gave a very wide range of end week, while the 10% difference limit varied only by ±1.5 weeks. This is about the same range that was reported from the long-term series at the mixed deciduous forest in Harvard USA (Braswell et al., 2005). The NPP limit gave an early end to the growing season, as the respiration is high in the autumn. Pilegaard et al. (2003) calculated the length of the growing season in Sorø based on a positive daily NEE limit; they found an average of 21 weeks, which is shorter than any of the estimates in this study.

Baldocchi et al. (2005) suggested that the time when the mean daily soil temperature equals the mean annual air temperature could be used as an indicator of the onset of the net carbon uptake of a deciduous forest. Using this criterion at the Sorø forest in 1999 they identified week 17 as the onset of net carbon uptake, which was close to the 4.7 °C limit. The start of the growing season in Hyytiälä and Norunda has been studied by Suni et al. (2003a, b), as a criterion they used the date when half-hourly values of NEE were first below 20% of the minimum summer value. This approach gave start weeks that were similar to the 5% limit in this study.

The total growing season length varied between 23 and 33 weeks in Hyytiälä, 24–38 weeks in Sorø and 24–40 weeks in Norunda. The relationship between the start, end and length of the growing season and total yearly NEE and GPP (Table 1) was tested for the different definitions (Table 3). For Hyytiälä the start of the growing season defined by the >4.7 °C criteria was best related to GPP ($R^2 = 0.54$) and NEE ($R^2 = 0.31$). The start of the growing season defined by the positive NPP criteria showed a good relationship to GPP in Sorø ($R^2 = 0.58$). For Norunda the end week defined by the NPP criterion could explain 37% of the between year variation in total GPP. The length of the growing season has been found to show good correlation to NEE between sites and has been suggested for use as a scaling parameter for NEE (Churkina et al., 2005). If the growing season length was the primary driver for carbon uptake, a relationship should also be seen between different years for a certain site. For a cool-temperate deciduous forest in Japan, an early and warm spring

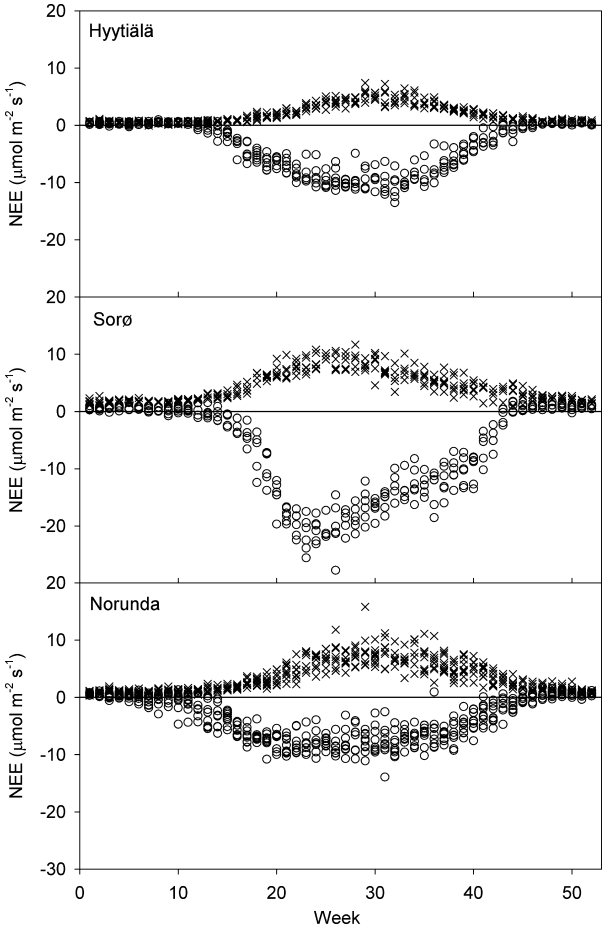

Fig. 4. Average NEE for night-time (×) and noon (10:00–14:00, ○) for 1-week periods for all years measured.

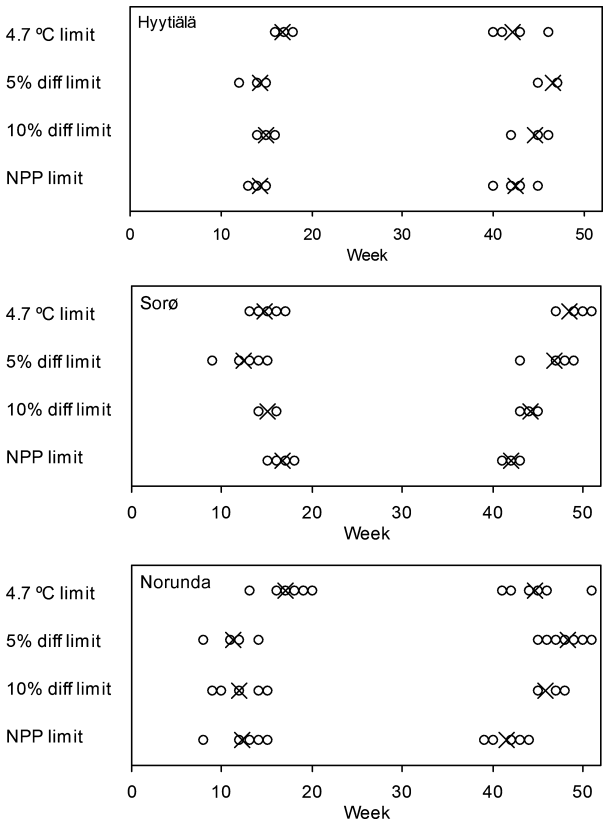

Fig. 5. Start and end week of the growing season determined with four different definitions based on: air temperature threshold, percentage differences between night-time and noon NEE (5 and 10%) and net primary productivity (NPP). Open circles show the yearly values and crosses the arithmetic mean.

had a positive effect on both annual NEE and GPP over a 9-yr study period (Saigusa et al., 2005), but such relationships were not found in this study. For Sorø there was actually significantly higher uptake (more negative NEE) for shorter growing seasons defined by the 5 and 10% of max criteria. For the El Niño events of 1983 and 1987 a decline in global terrestrial net primary productivity, that lagged 1 yr behind the events, was observed (Potter et al., 1999).

In all sites there were relationships between average summer maximum GPP and the total yearly GPP that was stronger than could be found for any of the values of the start and length of the growing season (Table 3, Fig. 6). This suggests that the interannual variation in GPP is more closely related to factors that affect the midseason photosynthetic capacity than the growing season length. In Sorø the years 2004 and 2005 had considerably higher GPP_{max} and total GPP than the other years. In 2004 there was high SWC during the whole season and there was no really high temperatures that could have limited photosynthesis. Urbanski et al. (2007) have demonstrated that unfavourable conditions can give negative consequences for GPP in subsequent years. But it is also reasonable to suppose that the build up of high photosynthetic capacity during a favourable year could be utilized the year after, which could explain high GPP in 2005. In Hyytiälä 2001 and 2003 had lower GPP_{max} and total GPP than the other years. One plausible reason for the decline in GPP_{max} in 2003 can be a drought in August 2002 and abnormal freezing in the soil in winter 2002–2003 due to exceptionally low soil water content. Another reason could be that the thinning in early 2002 had an effect on GPP even if it was not seen on the net flux (Vesala et al., 2005). The low value in 2001 is harder to explain, as it was a 'normal' year. In Norunda the years with highest GPP_{max} and total GPP, 1996 and 1998 both had ca. 5% higher than average SWC in July and August. SWC has also been identified as an important factor for explaining lower than average GPP in a deciduous forest in New England (Goulden et al., 1996) especially in the midsummer period (Urbanski et al., 2007).

4. Conclusions

The standard deviations of yearly total NEE and GPP were ca. 50 g C m^{-2} for all sites except GPP in Sorø, which was

Table 3. R^2 values for linear regressions between yearly total NEE or GPP and start, end and length (weeks) of the growing season with the four different definitions and also average maximum GPP from June to August calculated from the light response functions for 2000 μmol m^{-2} s^{-1} of PAR (see eq. 1)

	Hyytiälä		Sorø		Norunda	
	NEE	GPP	NEE	GPP	NEE	GPP
4.7 °C start	0.31	−0.54	−0.10	0.04	0.17	0.16
5% start	0.25	−0.07	−0.05	0.09	−0.09	0.00
10% start	0.27	−0.04	−0.71	−0.46	−0.18	0.02
NPP start	0.25	−0.04	−0.21	−0.58	−0.17	0.00
4.7 °C end	0.05	0.05	0.02	0.01	0.16	−0.13
5% end	0.32	−0.17	0.20	0.25	0.03	−0.34
10% end	0.55	−0.33	0.26	0.71	−0.23	0.00
NPP end	−0.06	0.08	0.10	0.07	−0.01	0.37
4.7 °C length	0.00	0.17	0.09	0.00	0.01	−0.22
5% length	−0.09	−0.01	0.61	0.05	0.23	−0.34
10% length	0.31	−0.27	0.70	0.72	0.03	−0.04
NPP length	−0.31	0.17	0.15	0.21	0.06	0.23
GPP max	−0.33	0.75	0.42	0.86	−0.04	0.70

A negative value means that there was a negative correlation.

129 g C m^{-2} (Table 1). In Sorø a favourable summer with no soil water stress was a possible explanation for considerably increased GPP for 2 yr. Temperature was the main controller of both respiration and photosynthesis outside the main growing season, while it was more complicated in summer with strong relationships between production capacity and respiration and a dependency of SWC for the interannual variation.

There is a high number of physical (frost events, drought, storm damage and snow breakage), biological (herbivores, reproduction efforts and deceases) and anthropogenic (thinning, fertilization, drainage, nitrogen deposition and air pollutions) factors that may affect the photosynthetic and respiration capacity of a forest ecosystem. To be able to reach a more complete understanding of interannual variability it is therefore important in future studies that not just the fluxes are measured but that the growing conditions of the forest are carefully documented. Notes of phenology, and a diary of daily observations of all kind of events and conditions that could have an impact on the ecosystem would be very useful.

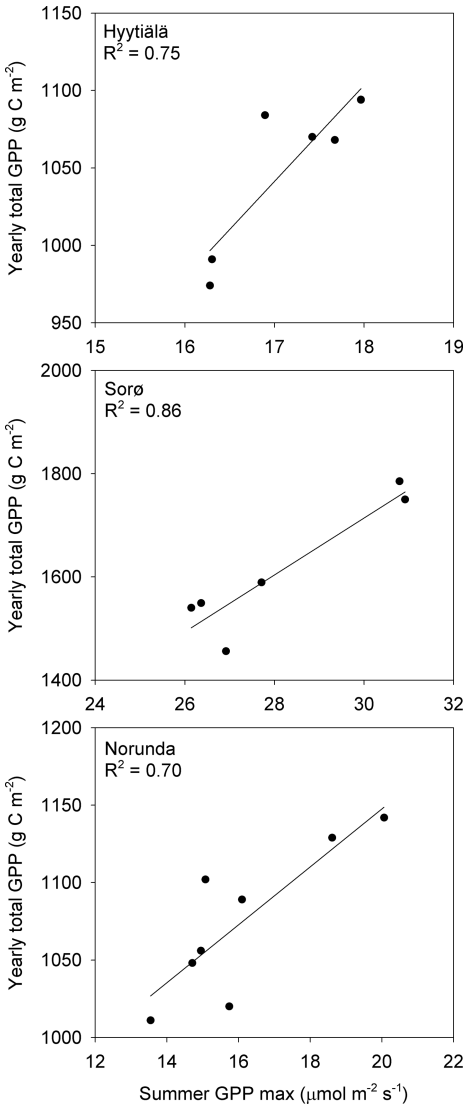

Fig. 6. The yearly total gross primary productivity (GPP) plotted against average maximum GPP from June to August calculated from the light response functions for 2000 μmol m^{-2} s^{-1} of PAR (see eq. 1).

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References

Ågren, G.I., Axelsson, B., Flower-Ellis, J.G.K., Linder, S., Persson, H., and co-authors. 1980. Annual carbon budget for a young Scots pine. In: *Structure and Function of Northern Coniferous Forests – An Ecosystem Study* Volume 32 (ed. T. Persson). *Ecological Bulletins* **32**, Stockholm, 307–313.

Aubinet, M., Grelle, A., Ibrom, A., Rannik, Ü., Moncrieff, J. and co-authors. 2000. Estimates of the annual net carbon and water exchange of forests: the EUROFLUX methodology. *Adv. Ecol. Res.* **30**, 113–175.

Baldocchi, D.D., Black, T.A., Curtis, P.S., Falge, E., Fuentes, J.D. and co-authors. 2005. Predicting the onset of net carbon uptake by deciduous forests with soil temperature and climate data: a synthesis of FLUXNET data. *Int. J. Biometeorol.* **49**, 377–387.

Baldocchi, D.D. and Harley, P.C. 1995. Scaling carbon dioxide and water vapour exchange from leaf to canopy in a deciduous forest. II. Model testing and application. *Special issue: Plant, Cell Environ.* **18**, 1157–1173.

Borken, W., Savage, K., Davidson, E.A. and Trumbore, S.E. 2006. Effects of experimental drought on soil respiration and radiocarbon efflux from a temperate forest soil. *Global Change Biol.* **12**, 177–193.

Braswell, B.H., Sacks, W.J., Linder, E. and Schimel, D.S. 2005. Esimating diurnal to annual ecosystem parameters by synthesis of a carbon flux model with eddy covariance net ecosystem exchange observations. *Global Change Biol.* **11**, 335–355.

Ceschia, E. 2001. *Environmental Effects on Spatial and Seasonal Variations of Stem Respiration in European Beech and Norway Spruce*. Doctoral Thesis, Silvestria 219. Swedish University of Agricultural Sciences, Uppsala.

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

Davidson, E.A. and Janssens, I. 2006. Temperature sensitivity of soil carbon decomposition and feedbacks to climate change. *Nature* **440**, 165–173.

Falge, E., Baldocchi, D.D., Olson, R., Anthoni, P., Aubinet, M. and co-authors. 2001. Gap filling strategies for defensible annual sums of net ecosystem exchange. *Agric. For. Meteorol.* **107**, 43–69.

Falge, E., Baldocchi, D., Tenhunen, J., Aubinet, M., Bakwin, P. and co-authors. 2002. Seasonality of ecosystem respiration and gross primary production as derived from FLUXNET measurements. *Agric. For. Meteorol.* **113**, 53–74.

Farquhar, G.D., von Caemmerer, S. and Berry, J.A. 1980. A biochemical model of photosynthetic CO_2 assimilation in leaves of C3 species. *Planta* **149**, 78–90.

Farquhar, G.D., von Caemmerer, S. and Berry, J.A. 2001. Models of photosynthesis. *Plant Physiol.* **125**, 42–45.

Goulden, M.L., Munger, J.W., Fan, S.-M., Daube, B.C. and Wofsy, S.C. 1996. Exchange of carbon dioxide by a deciduous forest: response to interannual climate variability. *Science* **271**, 1576–1578.

Grelle, A., Lindroth, A. and Mölder, M. 1999. Seasonal variation of boreal forest surface conductance and evoparation. *Agric. For. Meteorol.* **98–99**, 563–578.

Janssens, I.A., Lankreijer, H., Matteucci, G., Kowalski, A.S., Buchmann, N. and co-authors. 2001. Productivity overshadows temperature in determining soil and ecosystem respiration across European forests. *Global Change Biol.* **7**, 269–278.

Lagergren, F., Grelle, A., Lankreijer, H., Mölder, M. and Lindroth, A. 2006. Current carbon balance of the forested area in Sweden and its sensitivity to global change as simulated by Biome-BGC. *Ecosystems* **9**, 894–908.

Lindroth, A., Grelle, A. and Morén, A.-S. 1998. Long-term measurements of boreal forest carbon balance reveal large temperature sensitivity. *Global Change Biol.* **4**, 443–450.

Lindroth, A., Lagergren, F., Aurela, M., Bjarnadottir, B., Christensen, T. and co-authors. 2007. Leaf area index is the principal scaling parameter for both gross photosynthesis and ecosystem respiration of Northern deciduous and coniferous forests. *Tellus B*, doi:10.1111/j.1600-0870.2007.00330.x.

Lloyd, J. and Taylor, J.A. 1994. On the temperature dependency of soil respiration. *Funct. Ecol.* **8**, 315–323.

Lundin, L.-C., Halldin, S., Lindroth, A., Cienciala, E., Grelle, A. and co-authors. 1999. Continuous long-term measurements of soil-plant-atmosphere variables at a forest site. *Agric. For. Meteorol.* **98–99**, 53–73.

Lundmark, T., Bergh, J., Strand, M. and Koppel, A. 1998. Seasonal variation of maximum photochemical efficiency in boreal Norway spruce stands. *Trees-Struct. Funct.* **13**, 63–67.

Mäkelä, A., Kolari, P., Karimäki, J., Nikinmaa, E., Perämäki, M. and co-authors. 2006. Modelling five years of weather-driven variation of GPP in a boreal forest. *Agric. For. Meteorol.* **139**, 382–398.

Markkanen, T., Rannik, Ü., Keronen, P., Suni, T. and Vesala, T. 2001. Eddy covariance flux over a Scots pine forest. *Boreal Environ. Res.* **6**, 65–78.

Orchard, V.A. and Cook, F.J. 1983. Relationship between soil respiration and soil-moisture. *Soil Biol. Biochem.* **15**, 447–453.

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

Potter, C.S., Klooster, S. and Brooks, V. 1999. Interannual variability in terrestrial net primary production: exploration of trends and controls on regional to global scales. *Ecosystems* **2**, 36–48.

Randersson, J.T., Field, C.B., Fung, I.Y. and Tans, P.P. 1999. Increase in early season ecosystem uptake explain recent changes in the seasonal cycle of atmospheric CO_2 at high northern latitudes. *Geophys. Res. Lett.* **26**, 2765–2768.

Reichstein, M., Rey, A., Freibauer, A., Tenhunen, J., Valentino, R. and co-authors. 2003. Modeling temporal and large-scale spatial variability of soil respiration from soil water availability, temperature and vegetation productivity indices. *Global Biogeochem. Cycles* **17**, 1104, doi:10.1029/2003GB002035.

Ryan, M.G. and Law, B.E. 2005. Interpreting, measuring and modeling soil respiration. *Biogeochemistry* **73**, 3–27.

Saigusa, N., Yamamoto, S., Murayama, S. and Kondo, H. 2005. Interannual variability of carbon budget components in an AsiaFlux forest site estimated by long-term flux measurements. *Agric. For. Meteorol.* **134**, 4–16.

Suni, T., Berninger, F., Markkanen, T., Keronen, P., Rannik, Ü. and co-authors. 2003a. Interannual variability and timing of growing-season CO_2 exchange in a boreal forest. *J. Geophys. Res.* **108**(D9), 4265, doi:10.1029/2002JD002381.

Suni, T., Berninger, F., Vesala, T., Markkanen, T., Hari, P. and co-authors. 2003b. Air temperature triggers the recovery of evergreen boreal forest photosynthesis in spring. *Global Change Biol.* **9**, 1410–1426.

Thornton, P.E. 1998. *Regional Ecosystem Simulation: Combining Surface- and Satellite-Based Observations to Study Linkages Between Terrestrial Energy and Mass Budgets*. Doctoral Thesis. University of Montana, Missoula MT.

Urbanski, S., Barford, C., Wofsy, S., Kucharik, C., Pyle, E. and co-authors. 2007. Factors controlling CO_2 exchange on timescales from hourly to decadal at Harvard Forest. *J. Geophys. Res.* **112**, G02020, doi:10.1029/2006JG000293.

Valentini, R., Matteucci, G., Dolman, A.J., Schulze, E.-D., Rebmann, C. and co-authors. 2000. Respiration as the main determinant of carbon balance in European forests. *Nature* **404**, 861–865.

Vesala, T., Suni, T., Rannik, Ü., Keronen, P., Markkanen, T. and co-authors. 2005. Effect of thinning on surface fluxes in a boreal forest. *Global Biogeochem. Cycles* **19**, GB2001, doi:10.1029/2004GB002316.

Widén, B. and Majdi, H. 2001. Soil CO_2 efflux and root respiration at three sites in a mixed pine and spruce forest: seasonal and diurnal variation. *Can. J. For. Res.* **31**, 786–796.