

# Net primary production and light use efficiency in a mixed coniferous forest in Sweden

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## ABSTRACT

Simple light use efficiency ( $\epsilon$ ) models of net primary production (NPP) have recently been given great attention ( $\text{NPP} = \epsilon \times \text{absorbed photosynthetically active radiation}$ ). The underlying relationships have, however, not been much studied on a time step less than a month. In this study daily NPP was estimated as the sum of net ecosystem exchange (NEE) and heterotrophic respiration ( $R_h$ ) of a mixed pine and spruce forest in Sweden. NEE was measured by eddy correlation technique and  $R_h$  was estimated from measurements of forest floor respiration ( $R_f$ ) and the root share of  $R_f$ . The total yearly NPP was on average  $810 \text{ g C m}^{-2} \text{ year}^{-1}$  for 3 years and yearly  $\epsilon$  was between 0.58 and  $0.71 \text{ g C MJ}^{-1}$ , which is high in comparison with other studies. There was a seasonal trend in  $\epsilon$  with a relatively constant level of approximately  $0.90 \text{ g C MJ}^{-1}$  from April to September. Daily NPP did not increase for daily intercepted radiation above  $6 \text{ MJ m}^{-2} \text{ d}^{-1}$ , indicating that between-years variation in NPP is not directly dependent on total  $Q_i$ . The light was most efficiently used at an average daytime temperature of around  $15 \text{ }^\circ\text{C}$ . At daytime vapour pressure deficit above  $1400 \text{ Pa}$   $\epsilon$  was reduced by approximately 50%.

**Key-words:** light saturation; meteorological dependency; Norway spruce; Scots pine; seasonal variation.

## INTRODUCTION

Ecosystem net primary production (NPP) is an important characteristic that distinguishes different biomes and is useful for food and wood production estimates and for carbon budgets. In the past, carbon budgets and estimates of NPP have mostly been calculated on a yearly basis. Recent technological developments in continuous measurements of net ecosystem exchange (NEE), soil carbon fluxes and tree compartment fluxes have made it possible to make NPP estimates with a daily time resolution. The short time responses to environmental variables have to be estab-

lished in order to model the behaviour of ecosystems in a future changing climate as most processes are non-linear.

The development of remote sensing from satellites has showed potential for estimates of NPP (Ruimy, Saugier & Dedieu 1994; Potter, Klooster & Brooks 1999; Seaquist, Olsson & Ardö 2003). The most commonly used concept is to estimate NPP from the amount of absorbed photosynthetically active radiation ( $Q_a$ ) and a constant light use efficiency,  $\epsilon$  (Monteith 1972).

$$\text{NPP} = Q_a \epsilon \quad (1)$$

It is evolutionarily valid that  $Q_a$  will be related to NPP, as plants have no benefit of harvesting more light than they have resources to use (Field, Randerson & Malmstrom 1995). Satellite images can be used to derive  $Q_a$  by the use of a vegetation index (Asrar *et al.* 1984). The value of  $\epsilon$  was initially considered as relatively constant but substantial differences have been found that depend on ecosystem type, age, species composition, fertility and stresses (Ruimy *et al.* 1994; Goetz & Prince 1996; Gower, Kucharik & Norman 1999),  $\epsilon$  is therefore a crucial parameter to estimate. There have been several attempts to model seasonal variation in  $\epsilon$ , mainly as a function of air temperature, vapour pressure deficit and soil water deficit (e.g. Waring *et al.* 1995; Potter *et al.* 1999) but the relationships have mostly been based on assumptions from the literature and not verified by field studies.

There are three main methods to estimate NPP from field experiments: (1) from measurements of the different constitutions of the biomass produced, namely the above- and below-ground growth and litter production. Continuous measurements are however, difficult to achieve, especially for the below-ground part. (2) From the difference between gross assimilation and total autotrophic respiration measured by gas exchange. The great challenge in this method is to scale up from samples of single branches, roots and stem segments to the entire forest. (3) From the sum of NEE and heterotrophic respiration ( $R_h$ ). The integrated NEE can be relatively easily and accurately measured by the eddy correlation technique and  $R_h$  can be measured by trenching or root exclusion, by isotope technique or indirectly as the difference between soil efflux and root respiration (Hanson *et al.* 2000). One problem with the method

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is that the source area of the NEE varies with wind speed and wind direction and that NEE and  $R_h$  are not measured on the same scale. A scatter in the results can therefore be expected depending on the heterogeneity of the forest. Another problem is that NEE is small in relation to NPP on an annual basis, especially in old stands where respiration can even exceed assimilation (Lindroth, Grelle & Morén 1998). Consequently, the annual NPP will, to a large extent, depend on  $R_h$  and as measurements of soil respiration are generally biased to a various degree (Lund *et al.* 1999) there will be an uncertainty in the yearly NPP estimates.

Daily values of gross primary production (GPP) can be estimated directly from eddy correlation measurements of NEE by subtracting the total ecosystem respiration, estimated from the night-time flux relationship to temperature. This method has been used to evaluate daily variation in GPP and GPP light use efficiency (Turner *et al.* 2003). To our knowledge, daily variation in ecosystem NPP and the corresponding  $\epsilon$  has not been analysed before.

In the present study NPP and  $\epsilon$  were estimated according to method (3) as described above. NEE,  $Q_a$ , soil efflux and the fraction of root respiration to the total soil efflux were measured over the course of a season in a forest in central Sweden. The aim of the study was to evaluate how NPP and  $\epsilon$  varied over the year in relation to seasonal trends and meteorological variables. A simple model of  $\epsilon$  was developed and used to estimate daily NPP. The model was calibrated on data from 1999 and tested on the two preceding years.

## MATERIALS AND METHODS

### General methodology

The light extinction coefficient was estimated in seven different stands from leaf area index and measurements of radiation above and below the canopy. The mean extinction coefficient was used to calculate the amount of absorbed radiation for the forest within 300 m radius from the flux tower where NEE was measured. NPP was estimated from

NEE and heterotrophic respiration ( $R_h$ , positive values of NEE and NPP represent an uptake of C by the vegetation).

$$\text{NEE} = \text{NPP} - R_h \quad (2)$$

$R_h$  was estimated from measurement of forest-floor respiration ( $R_f$ ), for which a relationship was established with soil temperature (Widén 2001), and the fraction of soil  $\text{CO}_2$  efflux from roots ( $F_r$ ) (Widén & Majdi 2001) [ $R_h = R_f(1 - F_r)$ ].

### Measurement site

The measurements were made in the forest around the Norunda flux tower in central Sweden (60°5' N, 17°29' E, 45 m a.s.l). Scots pine (*Pinus sylvestris* L.) and Norway spruce [*Picea abies* (L.) Karst.] are the dominant tree species with a small fraction of deciduous trees, mainly *Betula pubescens* Ehrh., *B. pendula* Ehrh. and *Alnus glutinosa* (L.) Gaertn. The soil is a sandy glacial till with moderate to high occurrence of large boulders. Stands of varying species composition and age can be found within 1 km from the tower. The leaf area index (LAI) is between 3 and 6 with the higher values for stands dominated by spruce. The stands within 300 m from the tower are about 100 years old but differ in soil properties and species composition in both the tree and forest floor vegetation (Table 1). More details about the site can be found in Lundin *et al.* (1999).

### Light interception

The flux density of photosynthetic active radiation (PAR) above the canopy ( $Q$ ) was measured in the Norunda central tower at a height of 98 m with a Li-190SZ (Li-Cor Inc., Lincoln, NE, USA) sensor. Other meteorological variables were also measured in the tower (Lundin *et al.* 1999). PAR below the canopy ( $Q_b$ ) was measured in six satellite stands with different characteristics within 1 km from the tower (Table 1). Measurements were conducted in a plot of 40 m × 40 m or 40 m × 30 m within each stand. The measurements were made between 8 July and 21 September

**Table 1.** Stand description and measurements accomplished for the six satellite stands (Lundblad & Lindroth 2002), the plot measured in 2001 and the mean for the area within 300 m from the flux tower

Units	Age (years)	BA (m <sup>2</sup> ha <sup>-1</sup> )	P/S/D (%)	Tree density (trees ha <sup>-1</sup> )	LAI (m <sup>2</sup> m <sup>-2</sup> )	$Q_i$	NEE	$R_f$	$F_r$
North-east (NE)	90	27.1	90/1/9	906	3.99	x			
North (N)	34	18.7	71/27/2	971	3.84	x		x	x
North-west (NW)	110	48.6	66/32/2	669	5.41	x		x	x
South-west (SW)	50	28.6	53/47/0	794	5.02	x		x	
South (S)	105	35.8	59/38/4	700	5.17	x		x	x
South-east (SE)	60	24.1	7/93/0	1042	5.59	x			
Plot A	95	40.5	47/53/0	789	5.61	x			
300 m radius	100	39.3	63/33/5	870	4.34		x		

Stand description: age; BA, basal area at 1.3 m height; P/S/D, fraction of BA for pine, spruce and deciduous trees; tree density; and LAI, leaf area index from LAI-2000. Measurements: light interception ( $Q_i$ ), net ecosystem exchange (NEE), soil  $\text{CO}_2$  efflux ( $R_f$ ) and root share of  $R_f$  ( $F_r$ ).

1998. A 1-m-long ramp with three PAR sensors (Li-190SZ) placed approximately 50 cm above the ground was moved between the stands; each stand was measured during two periods of 3 to 8 days. Data were logged every 30 s and 5 min mean values were stored in a Campbell CR10 data logger (Campbell Scientific Inc., Logan, UT, USA). The LAI was estimated with a LAI-2000 plant canopy analyser (Li-Cor Inc.). In each of the six stands LAI was measured on two to six occasions between 24 July and 15 September in 1998, on 10 points in each stand. As no significant trend over time was found, the arithmetic means of the measured values were used (Table 1).

In addition,  $Q_b$  was measured in a stand 150 m southwest from the tower (Plot A, Table 1) in 2001 between 15 August and 25 October. Twenty-four sensors (JYP 1000; SDEC France, Reignac Sur Indre, France) were placed randomly over an area of about 40 m × 40 m. The sensors were logged every 20 s, and 5 min mean values were stored with a MiniCube VV data logger (Environmental Measuring Systems, Brno, Czech Republic). LAI in Plot A and in 12 additional plots within 300 m from the tower was measured in year 2001, also with the LAI-2000. Each plot was measured once, on approximately 25 points, and an average for the plots was calculated. All LAI-2000 measurements in this paper were corrected for clumping of needles with a correction factor of 1.65 (LAI-2000 Instruction Manual; Li-Cor Inc.).

For each day the quotient of the sum of the average PAR below ( $Q_b$ ) and the summed PAR above ( $Q$ ) the canopy was calculated. This quotient and LAI for the measured stand were used in the Beer–Lambert law to calculate the light extinction coefficient ( $k$ ) for each day.

$$k = \ln(Q_b/Q) / -\text{LAI} \quad (3)$$

These values of  $k$  are therefore based on intercepted PAR ( $Q_i$ ) and not absorbed PAR. The difference is however, small for LAI above 1 (Prince 1991). Measurement of reflected PAR in the tower showed that it was fairly constant at around 2.5% of  $Q$  on a daily basis. As reflected PAR was not measured above the satellite stands and can be expected to vary,  $Q_i$  was used. There is also a small fraction (<1% of  $Q$ ) of the light penetrating the canopy that is reflected in the ground vegetation and thereafter absorbed by the canopy, which was neglected. As this effect slightly compensates for the light that is reflected in the canopy the total difference between  $Q_a$  and  $Q_i$  was around 2%. To obtain  $Q_i$  for the area that represented the NEE flux, an average value of  $k$  was computed which was used with the LAI for the stands within 300 m from the tower and  $Q$  to calculate  $Q_i$  for each day in 1997–1999:

$$Q_i = Q[1 - \exp(-\text{LAI } k)] \quad (4)$$

### Net primary production (NPP)

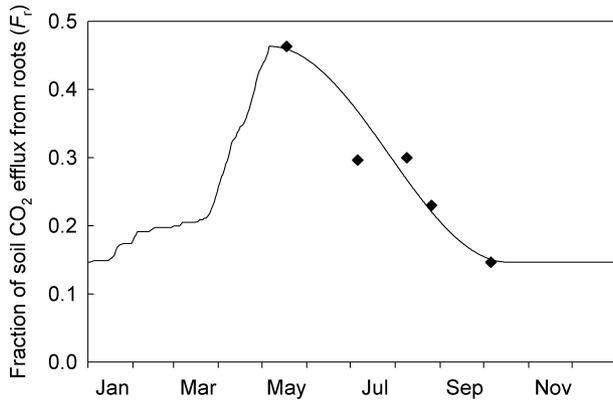
Net ecosystem exchange (NEE) was measured at a height of 35 m in the Norunda tower with a SOLENT three-dimensional sonic anemometer (Gill Instruments,

Lymington, UK) and a LI-6262 infrared gas analyser (Li-Cor Inc.). The sampling rate was 10 Hz and the fluxes were calculated based on 30 min averages. A detailed description of the system can be found in Grelle & Lindroth (1996). The eddy fluxes were corrected for sensor inclination, signal time lag caused by the length of the tube, frequency loss caused by tube attenuation and sensor response time (Leuning & Moncrieff 1990) and air density fluctuations because of sensible heat fluxes (Webb, Pearman & Leuning 1980). Data coverage was over 90% for all the years that are considered here. Soil temperature ( $T_s$ ) at 5 cm depth was measured in the six stands by thermocouples (105T; Campbell Scientific, Ltd. Shephed, UK); the average of the six stands was used in Eqn 5 below. Soil CO<sub>2</sub> efflux was measured in the six stands from September 1997 to August 1999 with a transparent open path chamber system (Iritz, Lindroth & Gårdenäs 1997; Morén & Lindroth 1999) that was moved between the stands (Widén 2001). The nocturnal mean values were used to obtain a relationship between forest-floor respiration ( $R_f$ ) and  $T_s$  for the four stands with mineral soil (excluding stands North-east and South-east that had peat soil):

$$R_f = 0.0085(T_s + 7.14)^{2.3} \quad (5)$$

The root respiration share of  $R_f$  ( $F_r$ ) was estimated on five occasions (17–19 May, 5–7 July, 8–10 August, 25–27 August and 5–7 October) in three of the six stands in 1999 (Widén & Majdi 2001). Root respiration was measured on excised roots in a chamber at ambient root temperature and soil CO<sub>2</sub> concentration, which is important for correct measurements (Hanson *et al.* 2000). Measurements were started within 30 min after excision; no decreasing trend was observed over time (B. Alstad (former Widén) personal comm. 2004) and cannot be expected during this time interval as the starch reserves can support root respiration for several weeks (Högberg *et al.* 2001). Before the roots were dug up,  $R_f$  was measured with a closed dark chamber system (Li-Cor 6000-09 chamber connected to a Li-Cor 6200 gas analyser; Li-Cor Inc.) on the same spots. At each occasion six spots were measured in each stand and the root respiration was scaled to area-based unit from root density that was measured in September 1998. Root biomass can vary over the season, which could have caused a systematic error in the  $F_r$  estimates. The measured  $F_r$  was on average 47% in the middle of May decreasing to 15% at the beginning of October (Fig. 1, symbols). It is a difficult task to measure  $F_r$  and the value varies over a wide range (10–90%) in different studies (Hanson *et al.* 2000). In a relatively poor pine forest in Northern Sweden, Högberg *et al.* (2001) found an average  $F_r$  value of 54% in a tree girdling experiment. A linear decrease of  $F_r$  from approximately 55% in the middle of May to 27% in the beginning of September can be interpreted from the results in a cool-temperate deciduous forest (Lee *et al.* 2003).

$F_r$  was modelled as a function of a cumulative temperature sum based on daytime average temperature, with a threshold of 0 °C. The accumulation of the temperature sum started on the first day of each year. When 350 day-



**Figure 1.** Fraction of total soil CO<sub>2</sub> efflux emerging from roots ( $F_r$ ) in 1999, measured values (diamonds, from Widén & Majdi 2001) and modelled (solid line).

degrees had been reached  $F_r$  was considered to be at the measured value in May (Fig. 1). Temperature sums are generally good predictors for triggering of biological cycles (Begon, Harper & Townsend 1990). The recovery of the photosynthetic capacity in the spring, which can be assumed to be related to the activity of the roots, has been successfully modelled with a temperature sum concept (Bergh, McMurtrie & Linder 1998). For best fit a half sine wave was adjusted from the date of 350 day-degrees to the date of the first autumn frost, to reach the measured value in October. This was followed by a constant value until next spring. The peak in May–June is associated with maximum rates of root growth and turnover in the annual cycle (Hanson *et al.* 1993).

Knowing the seasonal variation in  $F_r$ , NPP could be calculated as:

$$NPP = NEE + R_f(1 - F_r) \tag{6}$$

The daily value of the light use efficiency ( $\epsilon$ ) was then calculated as the quotient between the corresponding values of NPP and  $Q_i$ . NPP calculated this way is hereafter referred to as ‘measured’ although it depends on empirical relationships for the estimate of  $R_h$ . The seasonal variation in  $F_r$  is hard to interpolate from the measured occasions to the entire year, especially during winter and spring. However, since as much as 87–91% of the total NPP was produced between 18 May and 6 October the yearly totals were not sensitive to the exact level of  $F_r$  during winter and spring. Additionally, as the heterotrophic respiration is  $R_f(1 - F_r)$ , the estimate of NPP is not either too sensitive to  $F_r$  at low fractions; for example a value of 10 or 30% means just a 29% difference in heterotrophic respiration.

### Modelling the seasonal variation in $\epsilon$

In general, variation in  $\epsilon$  over time for an ecosystem depends mainly on temperature and soil water deficit (Potter *et al.* 1999). For cold climates, temperature is the dominant factor, reducing the photosynthesis and growth, especially in spring, far below the level that could be

expected from the radiation (Bergh *et al.* 1998). A simple model that was based mainly on temperature sums and frost events was developed to describe the variation in  $\epsilon$  with separate functions for the spring recovery and the autumn decline. A seasonal factor ( $f$ ) was calculated for each day (index  $d$ ). In the spring  $f$  was modelled as a function of a cumulative temperature sum ( $S_{spring}$ ) with a threshold of 0 °C:

$$f_d = \begin{cases} 1 & , S_{springd} \geq 100 \\ 1 - \frac{100 - S_{springd}}{100 + S_{springd}} & , S_{springd} < 100 \end{cases} \tag{7}$$

$$S_{springd} = \begin{cases} \frac{S_{springd-1} + T_{dayd}}{1 + P_{frostd}} & , T_{dayd} > 0 \\ \frac{S_{springd-1}}{1 + P_{frostd}} & , T_{dayd} \leq 0 \end{cases} \tag{8}$$

where  $T_{day}$  is the average daytime temperature and  $P_{frost}$  is a reduction factor for frost events:

$$P_{frost} = \begin{cases} 0 & , T_{min} \geq -3 \\ 0.05(-3 - T_{min})/5 & , -8 < T_{min} < -3 \\ 0.05 & , T_{min} \leq -8 \end{cases} \tag{9}$$

and  $T_{min}$  is the daily minimum temperature.

In the autumn the photosynthetic capacity is reduced by long-night-induced winter hardiness and frost events (Dormling 1993; Hollinger *et al.* 1999). Hence, during autumn  $f$  was calculated for each day as a combination of a negative temperature sum ( $S_{aut}$ ) with a threshold of 0 °C down to -50 day-degrees and an additive function of days from a starting date set to 10 August ( $D_{sum}$ ) as:

$$f_d = \begin{cases} 0 & , S_{autd} \leq -50 \\ \left(1 - \frac{D_{sumd}}{10000}\right) \left(1 + \frac{S_{autd}}{50}\right) & , S_{autd} > -50 \end{cases} \tag{10}$$

$$S_{autd} = \begin{cases} S_{autd-1} + T_{min} & , T_{min} < 0 \\ S_{autd-1} & , T_{min} \geq 0 \end{cases} \tag{11}$$

$$D_{sumd} = D_{sumd-1} + D_{DOYd} - 222 \tag{12}$$

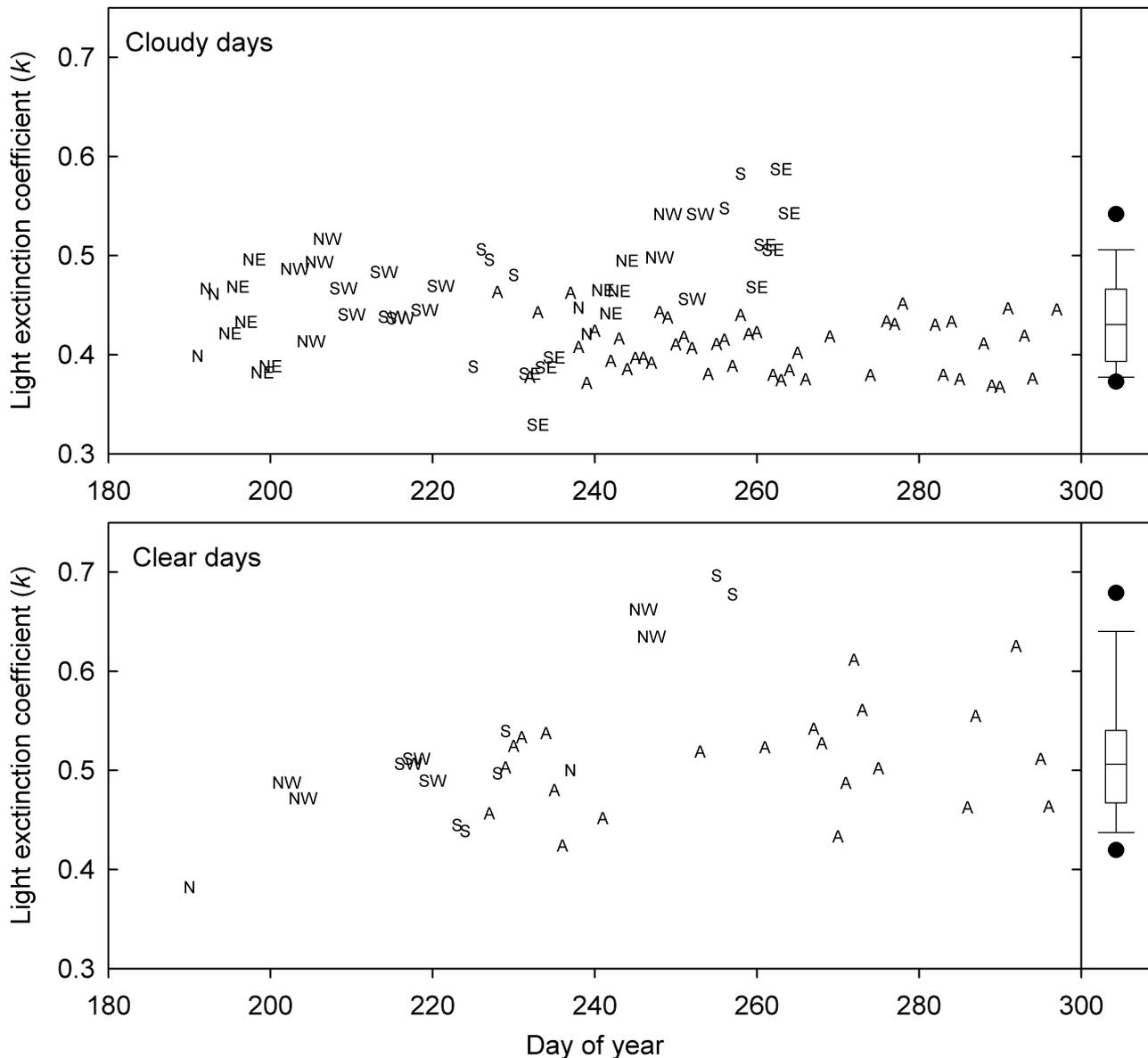
where  $D_{DOY}$  is the day number of the year. A linear regression between  $f$  and  $\epsilon$  was fitted to establish the relationship used in the final model. The  $\epsilon$ -values were calculated for periods which lengths were varied to have a total  $Q_i$  of 25 MJ m<sup>-2</sup>.

As  $F_r$  measurements were made in 1999 this year was used to establish the seasonal variation in  $\epsilon$ , and 1997 and 1998 were used for testing.

## RESULTS AND DISCUSSION

### Light extinction coefficient ( $k$ )

Plotting  $k$  over the measured period generated a large scatter. By splitting the data into ‘clear’ and ‘cloudy’ days, two more distinct sets of  $k$ -values were obtained (Fig. 2). Separating ‘clear’ and ‘cloudy’ days was done by fitting a line to the envelope of daily total radiation and setting a limit at 73% of the maximum. The limit was set after



**Figure 2.** The light extinction coefficient ( $k$ ) calculated for single days for seven different stands (see Table 1) with stand name as symbol. Plot A was measured in 2001 whereas the other stands were measured in 1998. The days were separated into clear and cloudy. To the right are box-plots of the distribution of  $k$ , showing the 5, 10, 25, 75, 90 and 95% percentiles and the median.

visual inspection of daily courses and setting a value above which clear conditions dominated. The mean  $k$  was 0.44 and 0.52 for the cloudy and clear days, respectively, with a significant difference ( $P < 0.001$ ). The difference between the data sets is most likely a result of different proportions of direct and diffuse radiation, which are absorbed at different ratios (Jarvis & Leverenz 1983). There were weak trends over the season for the two data sets that went in opposite directions. A decreasing trend for cloudy days could be a result of decreasing LAI. However, in 1998 no trend in LAI was found in the measurements that were ongoing until 15 September. In 2001 the light interception measurements continued until 21 October whereas LAI was only measured once. It is likely that

some needle shedding occurred during this period. An increasing trend for clear days is expected as a lower sun angle means a longer passage through the canopy for the direct radiation.

There was some variation in  $k$  between the stands (Table 2), but no relationship to the stand variables (Table 1) was found. The average  $k$ -values are within the range of earlier reports (Jarvis & Leverenz 1983), for example, 0.43 by Morén *et al.* (2000) (70-year-old Norway spruce and Scots pine mixture) and 0.69 by Sampson & Allen (1998) (14-year-old loblolly pine). An uncertainty in the estimated  $k$ -values lies in the correction for clumping of needles in the LAI estimate. The correction factor varies in relation to species and stand structure (Stenberg 1996). The

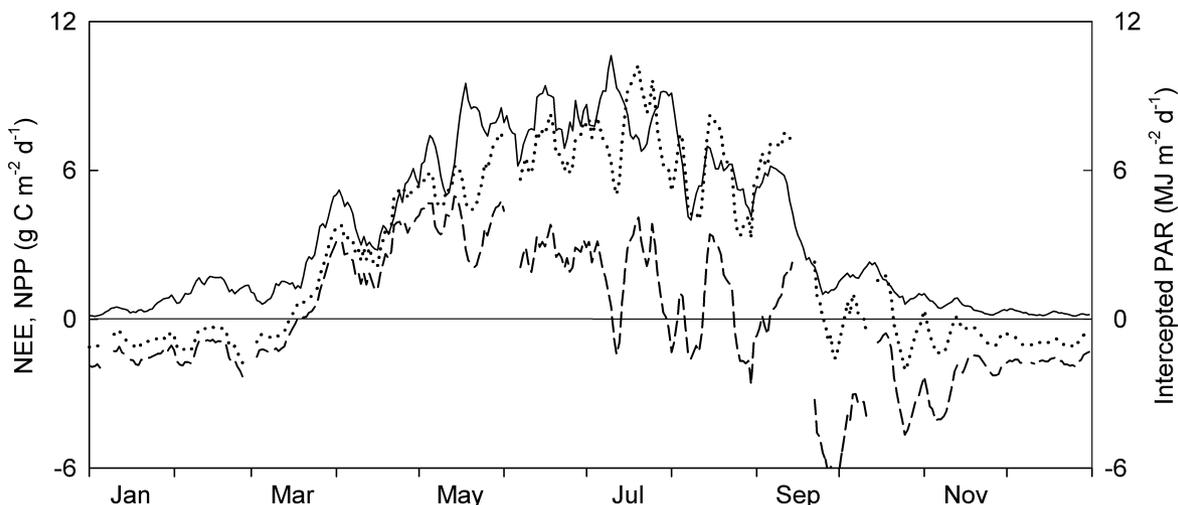


Figure 3. Seven-day running means of NEE (dashed line), NPP (dotted line) and  $Q_i$  (solid line) in 1999.

Table 2. The mean light extinction coefficient ( $k$ ) for the different stands divided into cloudy and clear days and the number of observed days ( $n$ )

	Cloudy		Clear		All	
	$k$	$n$	$k$	$n$	$k$	$n$
North-east	0.45	10	–	0	0.45	10
North	0.44	5	0.44	2	0.44	7
North-west	0.49	6	0.56	4	0.52	10
South-west	0.46	9	0.50	3	0.47	12
South	0.50	6	0.55	6	0.52	12
South-east	0.46	9	–	0	0.46	9
Plot A	0.41	46	0.51	22	0.44	68
Average all plots	0.46	7	0.51	5	0.47	7
Average all days	0.44	91	0.52	37	0.46	128

aim was, however, not to obtain exact values of  $k$  but rather to use  $k$  as an effective parameter to estimate  $Q_i$  for the stand around the tower. This estimate is insensitive to the correction factor as the stand around the tower had similar species composition as the average of the satellite stands for which  $k$  was estimated (Table 1). In the satellite stands there were only three sensors used, which is a small number, but as the variation in  $k$  was not larger than for stand A, where 24 sensors were used, the daily totals seem to have been sufficiently sampled.

**Net primary production (NPP) and intercepted radiation ( $Q_i$ )**

Plotting 7-d running means of NEE, NPP and  $Q_i$  shows that  $Q_i$  and NPP are related (Fig. 3). The coefficient of determination ( $r^2$ ) between NEE and  $Q_i$  was 0.43 and it was 0.70 between NPP and  $Q_i$  (Fig. 4). As the heterotrophic respiration ( $R_h$ ), that depends on soil temperature, is added to NEE and as  $Q$  and soil temperature are related ( $r^2 = 0.35$ ) there is some degree of multicollinearity,

which partly explains the stronger relationship to NPP. The maximum NPP was about  $16 \text{ g C m}^{-2} \text{ d}^{-1}$ , which was reached in the middle of July. Of this maximum value NEE contributed to 66%, and 34% was added from the estimate of  $R_h$ .

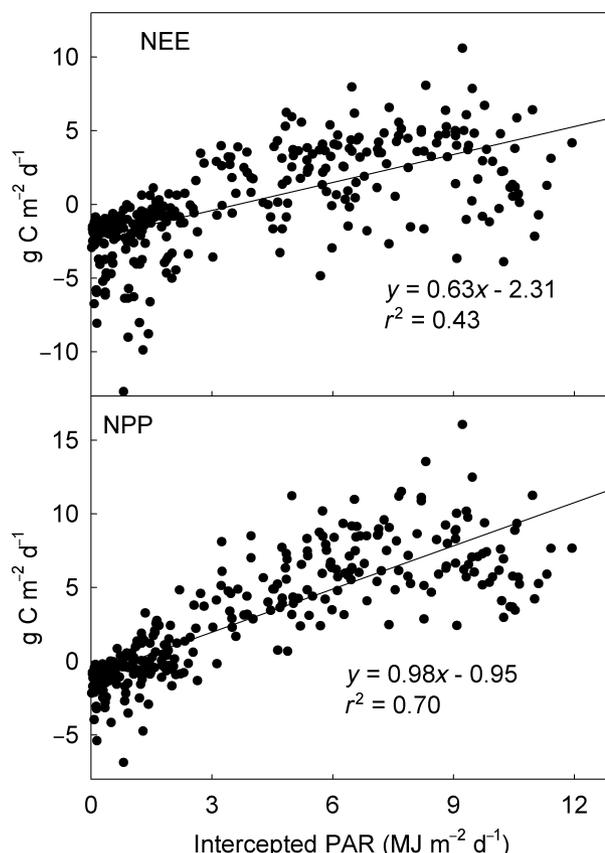
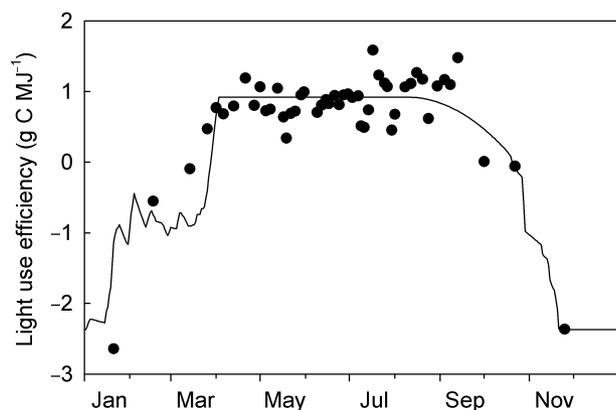


Figure 4. The relationship between NEE (above) and NPP (below) to intercepted PAR in 1999.



**Figure 5.** Measured (dots) light use efficiency ( $\epsilon$ ) calculated for periods with a total of  $25 \text{ MJ m}^{-2}$  of intercepted PAR and the modelled  $\epsilon$  (line) in 1999.

### Light use efficiency ( $\epsilon$ )

The plot of  $\epsilon$  over time showed a considerable scatter, especially during winter-time when it is the quotient between two small numbers. By calculating  $\epsilon$  for periods with a total  $Q_i$  of  $25 \text{ MJ m}^{-2}$  much of the scatter was reduced. The fit for the regression between the  $\epsilon$ -values and the seasonal factor  $f$  (Eqn 7 and 10) was:

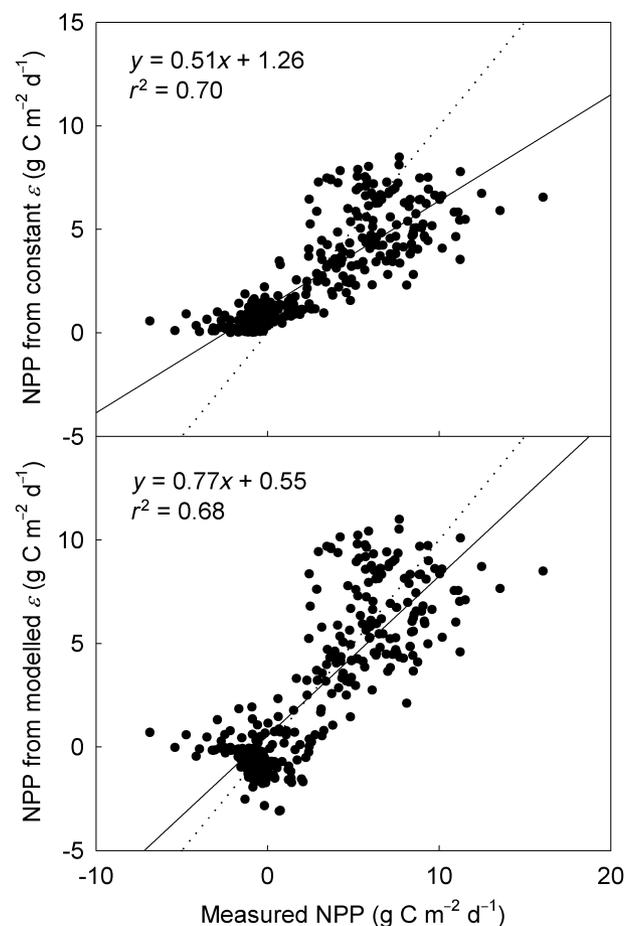
$$\epsilon_{\text{modelled}} = 3.29f - 2.37; \quad r^2 = 0.75.$$

This gives a maximum  $\epsilon_{\text{modelled}}$  of  $0.92 \text{ g C MJ}^{-1}$  (Fig. 5). During winter-time  $\epsilon$  becomes negative as a result of negative NPP. Negative NPP values in the winter are a consequence of higher autotrophic respiration than photosynthesis. There is, however, no reason for NPP to be negatively correlated to  $Q_i$  and a negative  $\epsilon$  has consequently no physical meaning. Actually NPP and  $Q_i$  have no relationship during this period and the model is only capable of giving a mean NPP for the period with negative  $\epsilon$ .

An annual value of  $\epsilon$  was also calculated from the yearly total of  $Q_i$  and NPP, respectively, which was  $0.71 \text{ g C MJ}^{-1}$  for 1999. The NPP value was replaced by the one estimated from the light use efficiency model for the days when NEE was missing, so that a yearly total could be estimated. The value is high, but within the range of values in other studies of similar ecosystems. Ruimy, Dedieu & Saugier (1996) have calculated a value of 0.44 for temperate evergreen needle-leaf forests. Higher values for high latitudes with relatively low amounts of yearly  $Q_i$ , as the present studied forest, can however, theoretically be expected (Medlyn

1998). With the assumption that 50% of the dry matter production is carbon, the value would be  $1.42 \text{ g dry matter MJ}^{-1}$  ( $\epsilon_{\text{total}}$ ). The value for the above ground production ( $\epsilon_{\text{above}}$ ) would be  $0.99 \text{ g dry matter MJ}^{-1}$  if 70% of the total NPP was above ground. Goetz & Prince (1996) reported  $\epsilon_{\text{above}}$  values between 0.17 and 0.89 for boreal black spruce (*Picea mariana*). In various conifer forests in Oregon, Runyon *et al.* (1994) reported  $\epsilon_{\text{above}}$  values between 0.18 and 0.92.

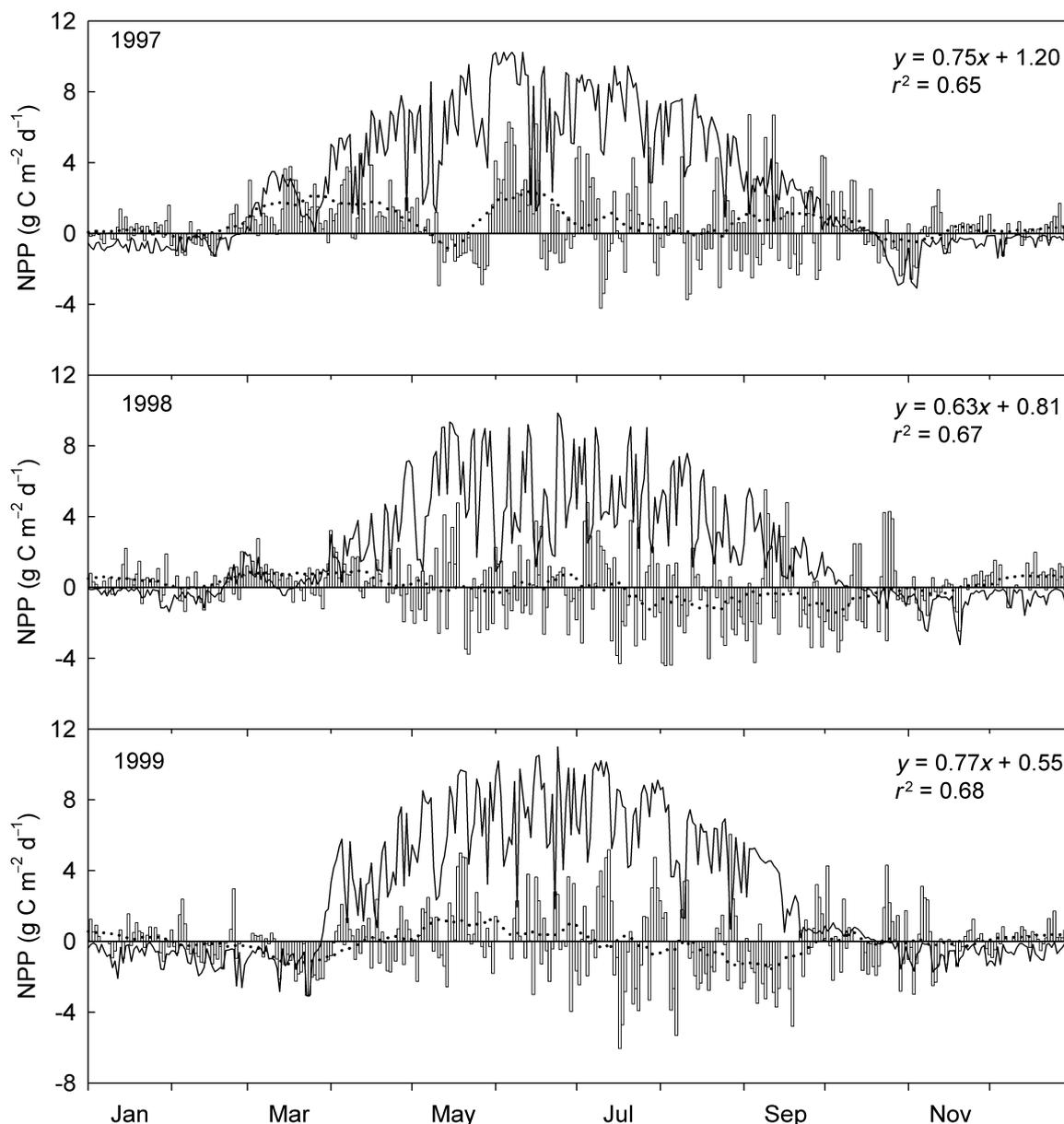
One reason for the difference between different estimates is that forest floor vegetation NPP may or may not be included. In the present approach the forest



**Figure 6.** Measured NPP against NPP from intercepted light and light use efficiency ( $\epsilon$ ) in 1999,  $\epsilon$  was either constant (above) or modelled (below). The solid lines are the regression result and the dotted lines are the 1 : 1 relationship.

**Table 3.** Total amount of intercepted PAR ( $Q_i$ ,  $\text{MJ m}^{-2} \text{ years}^{-1}$ ); total NPP ( $\text{g C m}^{-2} \text{ years}^{-1}$ ) from measurements, NPP calculated from  $Q_i$ , and the light use efficiency ( $\epsilon$ ), either constant from 1999 or modelled and the length of the growing season (GS, number of days with an average temperature above  $5^\circ \text{C}$  between 1 April and 31 October)

Year	$Q_i$	NPP measured	$\epsilon$	NPP const. $\epsilon$	NPP mod. $\epsilon$	GS (days)
1997	1348	775	0.57	957 (124%)	1006 (130%)	173
1998	1070	712	0.67	760 (107%)	729 (102%)	160
1999	1323	938	0.71	939 (100%)	918 (98%)	181



**Figure 7.** Modelled NPP based on light interception estimates for the years 1997–99 (solid line) and the difference between modelled and measured NPP (bars). The dotted lines show a 30-d running mean of the difference. The linear regression parameters with NPP measured as independent and NPP modelled as dependent variables are also given.

floor vegetation is included in NPP but since  $Q_i$  was estimated for the canopy only,  $\epsilon$  is overestimated. The assimilation of the forest floor has been estimated to be 19% of the total gross assimilation for a stand in the same forest (Morén 1999). With the assumption that the forest floor vegetation intercepts 80% of the light below the canopy the  $\epsilon$ -values are overestimated by approximately 12%.

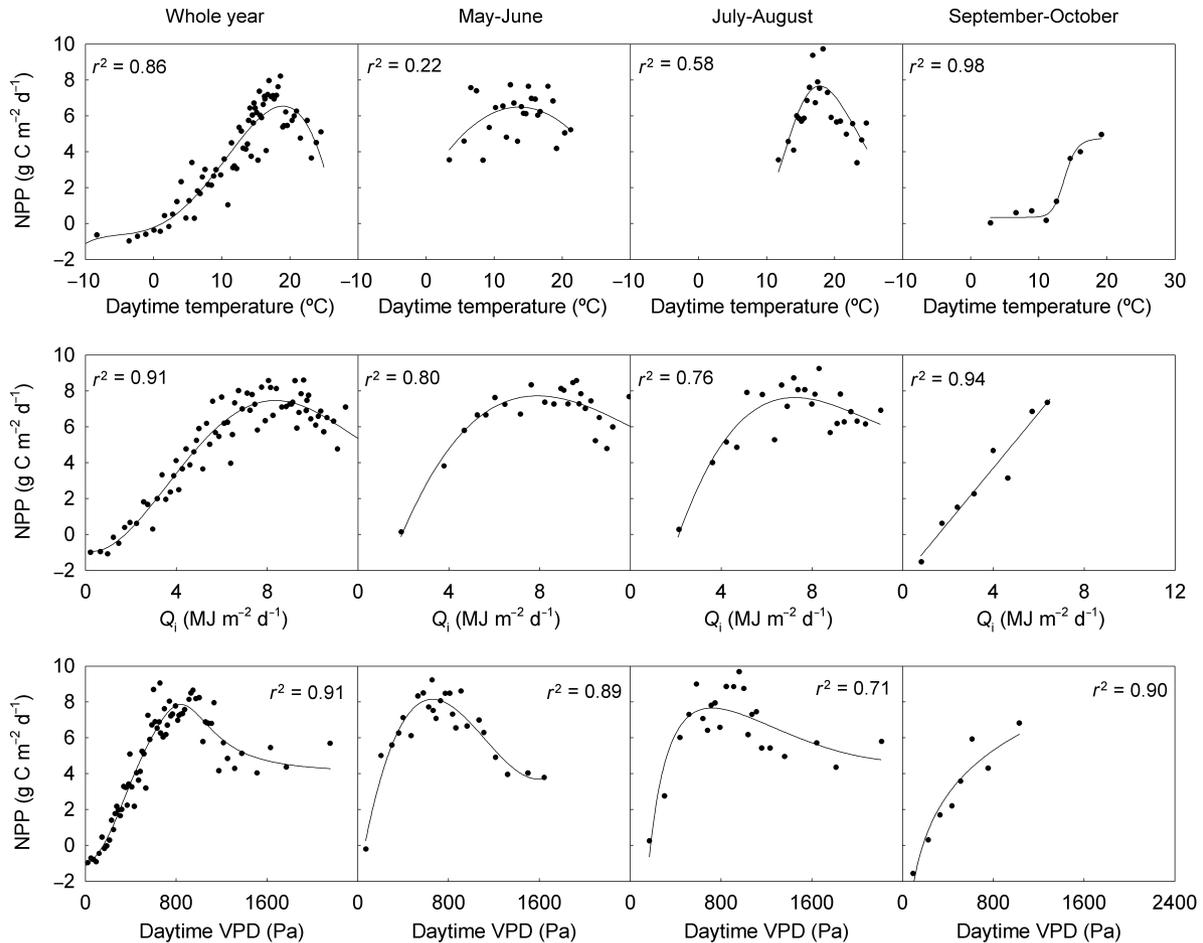
#### Between-year variation in annual NPP and $\epsilon$

The total measured NPP for the 3 years varied between 712 and 938 g C m<sup>-2</sup> year<sup>-1</sup> (Table 3) and  $\epsilon$  calculated from the

yearly totals varied between 0.57 and 0.71. A better relationship with yearly NPP was found for the length of the growing season than for total  $Q_i$ . As the relationship between  $Q_i$  and NPP is relatively weak (Fig. 4) it is reasonable that the number of days that contribute to the yearly NPP is of importance. NPP calculated from a variable  $\epsilon$  was not closer to the measured yearly totals than NPP calculated from a constant  $\epsilon$ .

#### Comparisons of seasonal NPP estimates

NPP computed from  $\epsilon_{\text{modelled}}$  did not explain more of the variation in measured NPP compared to NPP from using



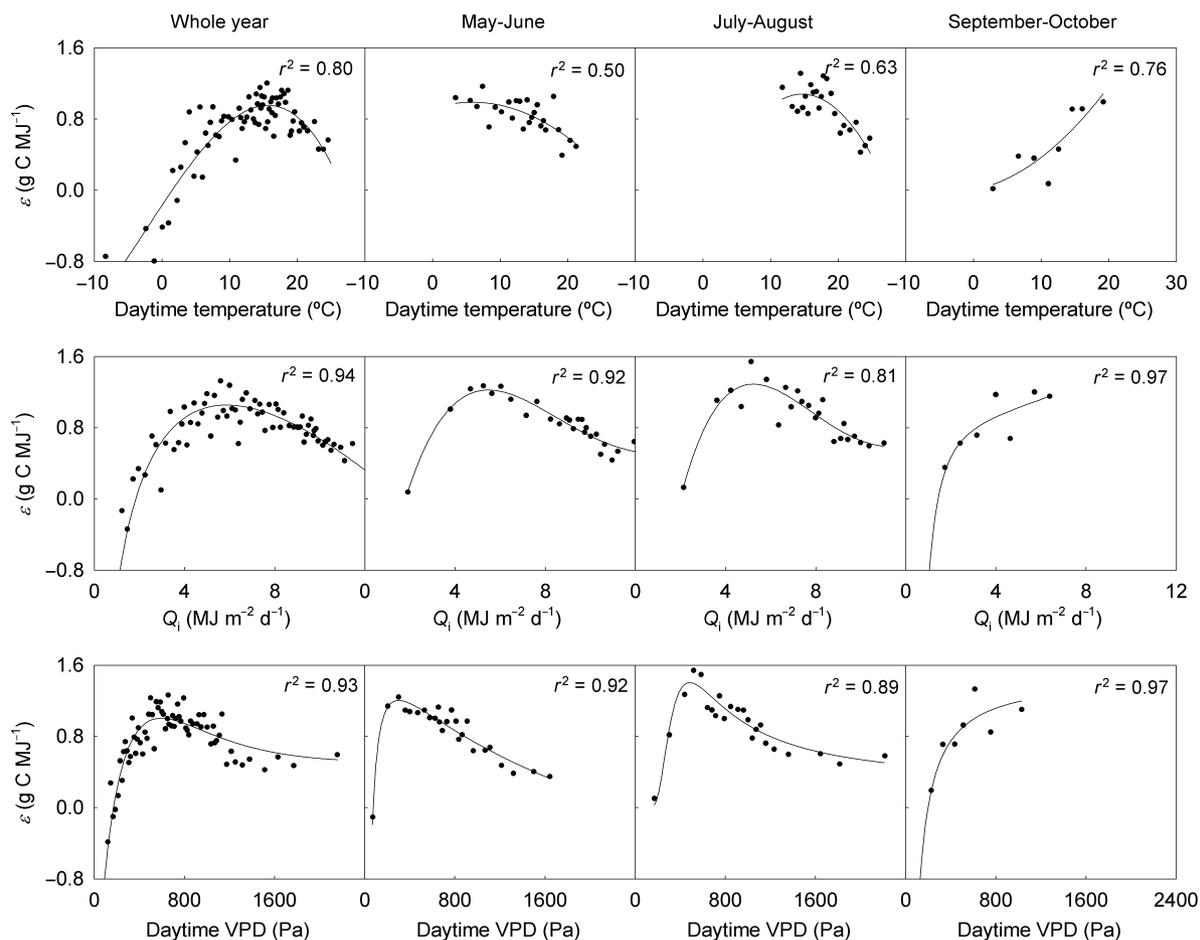
**Figure 8.** Average daytime air temperature, intercepted PAR ( $Q_i$ ) and average daytime vapour pressure deficit (VPD) plotted against net primary production (NPP). All three years are included in each plot but the growing season was divided into three periods. Averages were calculated for classes of the x-axis variable that was set to have a total  $Q_i$  of  $50 \text{ MJ m}^{-2}$ .

a constant  $\varepsilon$ , but the slope was closer to one and the intercept was closer to zero (Fig. 6). The light interception model performed similarly in explaining NPP for 1997 and 1998 as in the calibration year 1999 (Fig. 7). As expected, NPP is over or underestimated for days with radiation differing from the mean value in the winter and early spring as  $\varepsilon$  is used to calculate NPP, although there is no relationship between NPP and  $Q_i$  for this period. During spring NPP is systematically over or underestimated for some periods. It has been observed for several boreal sites that the commencement of photosynthesis in spring can be well predicted by a temperature sum whereas this failed for the present stand located just outside the southern limit of the boreal zone (Suní *et al.* 2003). Obviously, the present stand responds in a quicker way in both positive and negative direction to day-to-day variation in temperature in comparison with the more typical boreal sites. The period in the beginning of June in 1997, which starts with an abrupt change to warm and dry weather, is substantially overestimated.

### Relationships between NPP, $\varepsilon$ and weather parameters

In Figs 8 and 9 NPP and  $\varepsilon$  for all 3 years are plotted against average daytime temperature ( $T_{\text{day}}$ ), average daytime vapour pressure deficit ( $\text{VPD}_{\text{day}}$ ) and  $Q_i$ . The plots were divided into three periods: May–June, high light intensity and no water stress; July–August, high soil temperature and occasional soil water deficit; September–October, decreasing light and temperature, and the whole year. The NPP and  $Q_i$  data were sorted by the evaluated variable and average NPP and  $\varepsilon$  was calculated for ranges that was set to have a total  $Q_i$  of  $50 \text{ MJ m}^{-2}$ .

The NPP was highest at temperatures of approximately  $17\text{--}18^\circ\text{C}$  (Fig. 8) whereas the light was most efficiently used at approximately  $14\text{--}16^\circ\text{C}$  (Fig. 9). The relationship was weaker and with a lower optimum temperature in May–June than for the other periods. Seen over the whole year NPP was linearly related to  $Q_i$  between 1 and  $7 \text{ MJ m}^{-2} \text{ d}^{-1}$  but from May to August no positive relationship was found above  $5 \text{ MJ m}^{-2} \text{ d}^{-1}$ . The lack in increased NPP above



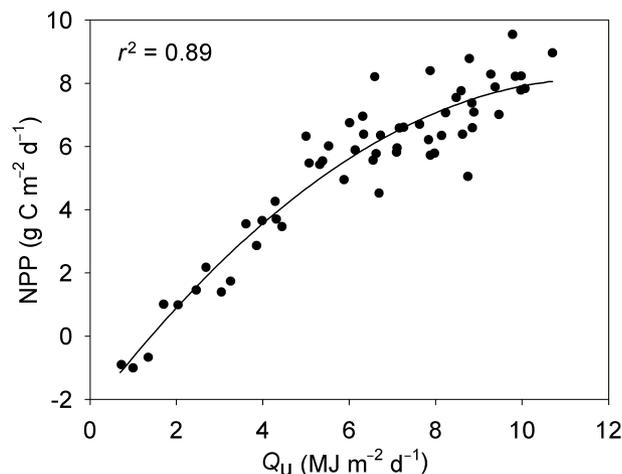
**Figure 9.** Average daytime air temperature, intercepted PAR ( $Q_i$ ) and average daytime vapour pressure deficit plotted against light use efficiency ( $\epsilon$ ). All three years are included in each plot but the growing season is divided in three periods.  $\epsilon$  was calculated for classes of the x-axis variable that were set to have a total  $Q_i$  of  $50 \text{ MJ m}^{-2}$ .

$5\text{--}7 \text{ MJ m}^{-2} \text{ d}^{-1}$  indicates that the needles begin to be light saturated. Turner *et al.* (2003) found a similar relationship with gross primary production for a boreal and a temperate forest whereas a tall grass prairie was linearly related to  $Q_i$  up to the maximum measured  $Q_i$  levels of  $11 \text{ MJ m}^{-2} \text{ d}^{-1}$ . The maximum photosynthetic capacity of conifers is generally low (Woodward & Smith 1994) and light saturation can be expected especially for stands with fairly low LAI. Another reason for a decreasing trend with increasing radiation is that the proportion of direct radiation increases. Gu *et al.* (2002) suggested that the diffuse and direct  $Q_i$  should be treated separately in NPP estimates as the diffuse radiation is more efficiently used. This could not be tested here because direct or diffuse radiation was not measured.

A light-saturation level for NPP also indicates that inter-annual variation in NPP may be insensitive to yearly total  $Q_i$ . The total abundant  $Q_i$  above  $6 \text{ MJ m}^{-2} \text{ d}^{-1}$  was 17, 11 and 18% of the yearly total for 1997, 1998 and 1999, respectively. If that amount is subtracted from the yearly  $Q_i$  (Table 3) new values of  $\epsilon$  can be calculated that would be 0.69, 0.75 and  $0.87 \text{ g C MJ}^{-1}$  for the 3 years, respectively.

The difference between 1997 and 1998 is thus reduced whereas 1999 is further accentuated. 1999 was a year with high temperatures in July and August leading to higher estimate of  $R_h$  than for the other years. The yearly total soil respiration may be insensitive to soil temperature (Giardina & Ryan 2000) and more dependent on substrate quality (Ågren & Bosatta 1996) and production (Janssens *et al.* 2001).

There is an intercept of the linear part in the  $Q_i$ -NPP relationship of  $-2.2 \text{ g C m}^{-2} \text{ d}^{-1}$  (Fig. 8) and as a result the  $Q_i$ - $\epsilon$  relationship deviates from the ideal constant level (Fig. 9).  $\text{VPD}_{\text{day}}$  had strong relationship to NPP with a maximum at approximately 600–800 Pa. The corresponding NPP- $\epsilon$  relationships show a very distinct negative correlation in the summer that reduces  $\epsilon$  to about half of the maximum value at approximately 1400 Pa, above which  $\epsilon$  reaches a plateau level. At high VPD stomata can be completely closed, which will stop the photosynthesis (Jarvis 1976; Stewart 1988) but with a daily time step a large part of the light can still be utilized as the maximum VPD is normally reached in the afternoon. In a light use efficiency model with an hourly time step a linear decrease in the



**Figure 10.** The utilized PAR ( $Q_u$ , see text), plotted against net primary production (NPP). All three years are included in the plot;  $\epsilon$  was calculated for classes of  $Q_u$  that were set to have a total  $Q_u$  of  $50 \text{ MJ m}^{-2}$ .

utilized light ( $Q_u$ ) was assumed between 1.5 and 2.5 kPa and no light utilized above 2.5 kPa (Waring *et al.* 1995). A similar approach was tested by assuming a linear decrease from 100 to 50% of  $Q_u$  between 0.5 and 1.5 kPa VPD<sub>day</sub> and constant levels of 100 and 50% below and above that span. No  $Q_u$  with  $T_{\text{day}}$  below  $0^\circ \text{C}$  was also assumed (Fig. 8 present paper, Waring *et al.* 1995). Figure 10 shows a positive quadratic relationship between  $Q_u$  and NPP up to the highest values of  $Q_u$  but a decreasing slope can still be observed for  $Q_u$  above  $6 \text{ MJ m}^{-2} \text{ d}^{-1}$ . Yearly total light use efficiency for  $Q_u$  would be 0.73, 0.79 and  $0.89 \text{ g C MJ}^{-1}$  for the 3 years, which is similar to the values found by subtracting the light above  $6 \text{ MJ m}^{-2} \text{ d}^{-1}$ .

## CONCLUSIONS

- 1 Using NEE measurements in combination with measurements of  $R_h$  is a useful method for assessment of  $\epsilon$ -models.
- 2 Part of the explanation to the rather high value of  $\epsilon$  obtained in this study,  $1.42 \text{ g dry matter MJ}^{-1}$ , can be attributed to the ground vegetation component. Including PAR absorbed by the ground vegetation gives a more reasonable  $\epsilon$ -value of  $1.27 \text{ g dry matter MJ}^{-1}$ .
- 3 The lack of correlation between NPP and absorbed PAR at high PAR will have implications for the estimation of annual carbon balances by the linear  $\epsilon$ -model. It is a risk that such models will overestimate the between-year variation in NPP.
- 4 The yearly total NPP was not better estimated with a seasonal varying  $\epsilon$ , but the seasonal variation was better described.
- 5 The results indicate that more accurate estimates of NPP can be calculated by including responses of  $\epsilon$  to low temperatures, high VPD and high light levels, but it could not be confirmed by a better estimate of the yearly total.

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## REFERENCES

- Ågren G.I. & Bosatta E. (1996) Quality: a bridge between theory and experiment in soil organic matter studies. *Oikos* **76**, 522–528.
- Asrar G., Fuchs M., Kanemasu E.T. & Hatfield J.L. (1984) Estimating absorbed photosynthetic radiation and Leaf Area Index from spectral reflectance in wheat. *Agronomy Journal* **76**, 300–306.
- Begon M., Harper J.L. & Townsend C.R. (1990) *Ecology: Individuals, Populations and Communities*. Blackwell Scientific Publications, Cambridge, MA, USA.
- Bergh J., McMurtrie R.E. & Linder S. (1998) Climatic factors controlling the productivity of Norway spruce: a model-based analysis. *Forest Ecology and Management* **110**, 127–139.
- Dormling I. (1993) Bud dormancy, frost hardiness, and frost drought in seedlings of *Pinus sylvestris* and *Picea abies*. In *Advances in Plant Cold Hardiness* (eds P.H. Li & L. Christerson), pp. 285–298. CRC Press, Boca Raton, FL, USA.
- Field C.B., Randerson J.T. & Malmstrom C.M. (1995) Global net primary production – combining ecology and remote sensing. *Remote Sensing of Environment* **51**, 74–88.
- Giardina C.P. & Ryan M.G. (2000) Evidence that decomposition rates of organic carbon in mineral soil do not vary with temperature. *Nature* **404**, 858–861.
- Goetz S.J. & Prince S.D. (1996) Remote sensing of net primary production in boreal forest stands. *Agricultural and Forest Meteorology* **78**, 149–179.
- Gower S.T., Kucharik C.J. & Norman J.M. (1999) Direct and indirect estimation of leaf area index,  $f$  (APAR), and net primary production of terrestrial ecosystems. *Remote Sensing of Environment* **70**, 29–51.
- Grelle A. & Lindroth A. (1996) Eddy-correlation system for long-term monitoring of fluxes of heat, water vapour and  $\text{CO}_2$ . *Global Change Biology* **2**, 297–307.
- Gu L.H., Baldocchi D., Verma S.B., Black T.A., Vesala T., Falge E.M. & Dowty P.R. (2002) Advantages of diffuse radiation for terrestrial ecosystem productivity. *Journal of Geophysical Research-Atmospheres* **107**(D6), 4050, doi: 10.1029/2001JD001242.
- Hanson P.J., Edwards N.T., Garten C.T. & Andrews J.A. (2000) Separating root and soil microbial contributions to soil respiration: a review of methods and observations. *Biogeochemistry* **48**, 115–146.
- Hanson P.J., Wullschleger S.D., Bohlman S.A. & Todd D.E. (1993) Seasonal and topographic patterns of forest floor  $\text{CO}_2$  efflux from an upland oak forest. *Tree Physiology* **13**, 1–15.
- Högberg P., Nordgren A., Buchmann N., Taylor A.F.S., Ekblad A., Hogberg M.N., Nyberg G., Ottosson-Lofvenius M. & Read D.J. (2001) Large-scale forest girdling shows that current photosynthesis drives soil respiration. *Nature* **411**, 789–792.
- Hollinger D.Y., Goltz S.M., Davidson E.A., Lee J.T., Tu K. & Valentine H.T. (1999) Seasonal patterns and environmental control of carbon dioxide and water vapour exchange in an ecotonal boreal forest. *Global Change Biology* **5**, 891–902.
- Iritz Z., Lindroth A. & Gärdenäs A. (1997) Open ventilated chamber system for measurements of  $\text{H}_2\text{O}$  and  $\text{CO}_2$  fluxes from the soil surface. *Soil Technology* **10**, 169–184.
- Janssens I.A., Lankreijer H., Matteucci G., *et al.* (2001) Productivity overshadows temperature in determining soil and ecosystem

- respiration across European forests. *Global Change Biology* **7**, 269–278.
- Jarvis P.G. & Leverenz J.W. (1983) Productivity of temperate, deciduous and evergreen forests. In *Encyclopedia of Plant Physiology* (eds O.L. Lange, P.S. Nobel, C.B. Osmond & H. Ziegler) vol. 12d, pp. 233–280. Springer-Verlag, New York, USA.
- Jarvis P.G. (1976) The interpretation of the variations in leaf water potential and stomatal conductance found in canopies in the field. *Philosophical Transactions of the Royal Society of London, Series B* **273**, 593–610.
- Lee M.-S., Nakane K., Nakatsubo T. & Koizumi H. (2003) Seasonal changes in the contribution of root respiration to total soil respiration in a cool-temperate deciduous forest. *Plant and Soil* **255**, 311–318.
- Leuning R. & Moncrieff J.B. (1990) Eddy-covariance CO<sub>2</sub> flux measurements using open- and closed-path CO<sub>2</sub> analysers: corrections for analyser water vapour sensitivity and damping of fluctuations in air sampling tubes. *Boundary Layer Meteorology* **53**, 63–76.
- Lindroth A., Grelle A. & Morén A.-S. (1998) Long-term measurements of boreal forest carbon balance reveal large temperature sensitivity. *Global Change Biology* **4**, 443–450.
- Lund C.P., Riley W.J., Pierce L.L. & Field C.B. (1999) The effects of chamber pressurization on soil-surface CO<sub>2</sub> flux and the implications for NEE measurements under elevated CO<sub>2</sub>. *Global Change Biology* **5**, 269–281.
- Lundblad M. & Lindroth A. (2002) Stand transpiration and sap-flow density in relation to weather, soil moisture and stand characteristics. *Basic and Applied Ecology* **3**, 229–243.
- Lundin L.-C., Halldin S., Lindroth A., *et al.* (1999) Continuous long-term measurements of soil-plant-atmosphere variables at a forest site. *Agricultural and Forest Meteorology* **98–99**, 53–73.
- Medlyn B.E. (1998) Physiological basis of the light use efficiency model. *Tree Physiology* **18**, 167–176.
- Monteith J.L. (1972) Solar radiation and productivity in tropical ecosystems. *Journal of Applied Ecology* **9**, 747–766.
- Morén A.-S. (1999) *Carbon Dioxide and Water Exchange in a Boreal Forest in Relation to Weather and Season*. Silvestria 86 (Doctoral Thesis). Swedish University of Agricultural Sciences, Uppsala, Sweden.
- Morén A.-S. & Lindroth A. (1999) *Field Measurements of Water Vapour and Carbon Dioxide Fluxes-Chamber System and Climatic Monitoring by an Automatic Station*. Department for Production Ecology. Report 4. Swedish University of Agricultural Sciences, Uppsala, Sweden.
- Morén A.-S., Lindroth A., Flower-Ellis J., Cienciala E. & Mölder M. (2000) Branch transpiration of pine and spruce scaled to tree and canopy using needle biomass distributions. *Trees* **14**, 384–397.
- Potter C.S., Klooster S. & Brooks V. (1999) Interannual variability in terrestrial net primary production: Exploration of trends and controls on regional to global scales. *Ecosystems* **2**, 36–48.
- Prince S.D. (1991) A model of regional primary production for use with coarse-resolution satellite data. *International Journal of Remote Sensing* **12**, 1313–1330.
- Ruimy A., Dedieu G. & Saugier B. (1996) TURC: a diagnostic model of continental gross primary productivity and net primary productivity. *Global Biogeochemical Cycles* **10**, 269–285.
- Ruimy A., Saugier B. & Dedieu G. (1994) Methodology for the estimation of terrestrial net primary production from remotely sensed data. *Journal of Geophysical Research* **99**, 5263–5283.
- Runyon J., Waring R.H., Goward S.N. & Welles J.M. (1994) Environmental limits on net primary production and light use efficiency across the Oregon transect. *Ecological Applications* **4**, 226–238.
- Sampson D.A. & Allen H.L. (1998) Light attenuation in a 14-year-old loblolly pine stand as influenced by fertilization and irrigation. *Trees* **13**, 80–87.
- Seaquist J.W., Olsson L. & Ardö J. (2003) A remote sensing-based primary production model for grassland biomes. *Ecological Modelling* **169**, 131–155.
- Stenberg P. (1996) Correcting LAI-2000 estimates for the clumping of needles in shoots of conifers. *Agricultural and Forest Meteorology* **79**, 1–8.
- Stewart J.B. (1988) Modelling surface conductance of pine forests. *Agricultural and Forest Meteorology* **43**, 19–35.
- Sun T., Berninger F., Vesala T., *et al.* (2003) Air temperature triggers the recovery of evergreen boreal forest photosynthesis in spring. *Global Change Biology* **9**, 1410–1426.
- Turner D.P., Urbanski S., Bremer D., Wofsy S.C., Meyers T., Gower S.T. & Gregory M. (2003) A cross-biome comparison of daily light use efficiency for gross primary production. *Global Change Biology* **9**, 383–395.
- Waring R.H., Law B.E., Goulden M.L., Bassow S.L., McCreight R.W., Wofsy S.C. & Bazzaz F.A. (1995) Scaling gross ecosystem production at Harvard Forest with remote sensing: a comparison of estimates from a constrained quantum-use efficiency model and eddy correlation. *Plant, Cell and Environment (Special Issue: Scaling Up)* **18**, 1201–1213.
- Webb E.K., Pearman G.I. & Leuning R. (1980) Correction of flux measurements for density effects due to heat and water vapour transfer. *Quarterly Journal of the Royal Meteorological Society* **106**, 85–100.
- Widén B. (2001) CO<sub>2</sub> Exchange Within a Swedish Coniferous Forest, Spatial and Temporal Variation. Silvestria 184 (doctoral Thesis). Swedish University of Agricultural Sciences, Uppsala, Sweden.
- Widén B. & Majdi H. (2001) Soil CO<sub>2</sub> efflux and root respiration at three sites in a mixed pine and spruce forest: seasonal and diurnal variation. *Canadian Journal of Forest Research* **31**, 786–796.
- Woodward F.I. & Smith T.M. (1994) Predictions and measurements of the maximum photosynthetic rate,  $A_{max}$ , at the global scale. In *Ecophysiology of Photosynthesis* (eds E.-D. Schultze & M.M. Caldwell), pp. 491–509. Springer, Berlin, Germany.

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