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TELLUS

Leaf area index is the principal scaling parameter for both gross photosynthesis and ecosystem respiration of Northern deciduous and coniferous forests

By ANDERS LINDROTH[1]*, FREDRIK LAGERGREN[1], MIKA AURELA[2], BRYNHILDUR BJARNADOTTIR[1,3], TORBEN CHRISTENSEN[1], EBBA DELLWIK[4], ACHIM GRELLE[5], ANDREAS IBROM[6], TORBJÖRN JOHANSSON[1], HARRY LANKREIJER[1], SAMULI LAUNIAINEN[7], TUOMAS LAURILA[2], MEELIS MÖLDER[1], EERO NIKINMAA[8], KIM PILEGAARD[6], BJARNI D. SIGURDSSON[9] and TIMO VESALA[7], [1]*Geobiosphere Science Centre, Physical Geography and Ecosystems Analysis, Lund University, Lund, Sweden;* [2]*Finnish Meteorological Institute, Helsinki, Finland;* [3]*Icelandic Forest Research, Mogilsa, Iceland;* [4]*Wind Energy Department, Risoe National Laboratory, Risoe, Denmark;* [5]*Department of Ecology, Swedish University of Agricultural Sciences, Uppsala, Sweden;* [6]*Biosystems Department, Risoe National Laboratory, Risoe, Denmark;* [7]*Department of Physical Sciences, Helsinki University, Helsinki, Finland;* [8]*Department of Forest Ecology, Agricultural University Helsinki, Helsinki, Finland;* [9]*Agricultural University of Iceland, Reykjavik, Iceland*

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ABSTRACT

Data on net CO_2 exchange from eight forests in Denmark, Sweden, Finland and Iceland were used to analyse which factors were controlling photosynthesis and respiration. The forests consisted of different species ranging in climatic condition from temperate to subarctic. Only well mixed conditions were analysed ($u^* > 0.3$ m s^{-1}). The parameters of a light response function showed strong seasonal variations with similar behaviour for all stands except for a beech forest where the development of a vigorous ground vegetation in spring affected the photosynthesis parameters differently as compared to the other forests. The beech forest also showed the highest respiration rates in the earlier part of the growing season in contrast to the other forests that showed maximum values in late part of July. The mean half-monthly nighttime respiration rates were well explained by an equation with one fitting parameter, the respiration rate at 10 °C, with an $r^2 = 0.864$ for all stands together. The difference between the stands concerning both photosynthesis and respiration parameters were largely explained by the differences in LAI. After normalizing for LAI, the only remaining correlation was between respiration and stand age. These results are promising for application of remote sensing for estimation of respiration as well as gross primary productivity from forests.

1. Introduction

After more than a decade of studies of carbon fluxes from forests much new insight into the processes controlling the exchange of CO_2 has been gained. The timing of snowmelt and soil thaw (Goulden et al., 1998), the onset of warming in the spring (Black et al., 2000; Tanja et al., 2003) as well as other factors affecting phenology can have large impact on the annual carbon balance of a particular forest. The management and age of forests are another factors, which also are crucial for the carbon balance (Grace, 2001; Kowalski et al., 2004). When comparing different forests it is difficult to find unique factors that explain the difference in annual net ecosystem productivity (N_{ep}) (Black et al., 2005). Valentini et al. (2000) showed that, for European forests, latitude could best explain the variation in N_{ep} between the forests but they could not deduce which underlying factor was responsible for this latitudinal behaviour. The reason for the difficulty in understanding the difference in N_{ep} between forests is probably that N_{ep} is the small difference between two large terms; the gross photosynthesis (GPP) and the ecosystem respiration (R_{eco}). A small shift in either of these will have a large impact on the net balance. In addition, both GPP and R_{eco} depend in non-linear ways on several environmental variables, which make it difficult find unique explanatory factors. Therefore, in order to

*Corresponding author.
e-mail: anders.lindroth@nateko.lu.se
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understand differences between different forests it is probably more successful to try to understand the differences in the two separate components in the first instance.

We know from numerous studies that temperature exerts a strong control over respiration (e.g. Raich and Schlesinger, 1992; Lloyd and Taylor, 1994; Janssens et al., 2001) and to some degree also soil water content (Davidson et al., 1998; Sascha et al., 2005). The respiration increases exponentially with temperature but many studies have shown that the sensitivity to temperature, the Q_{10}, varies over the season with increasing sensitivity at lower temperatures (e.g. Tjoelker et al., 2001). The relationship between respiration and temperature is confounded by the respiration consisting of both plant and microbial respiration, which might have different Q_{10}s. In addition, the plant processes behind the autotrophic respiration may have different temperature responses since the processes varies over the season, and particularly the role of growth respiration which is dominant during the period of active growth. The dependency between ecosystem respiration and soil water content is less clear with data showing that the effect can be both positive and negative (Davidson et al., 1998). Other factors, such as soil pH and amount of living roots have also been shown to influence soil respiration (Sascha et al., 2005). Finally, the nitrogen availability in the soil has also been reported to have both positive and negative impact on soil respiration, decomposition and soil organic matter (Wallenstein et al., 2006; Hyvönen et al., 2007). The negative effect of nitrogen availability on decomposition and respiration may be mediated through its effect on substrate quality and hence on the microbial part of the ecosystem respiration (Ågren et al., 2001).

The biochemistry of photosynthesis has been studied extensively during decades and the processes are relatively well understood. Nitrogen availability, light, temperature, air humidity and water potential are primary factors controlling the gross photosynthesis at leaf level (e.g. Farquhar, 1989) and phenology, leaf area density and canopy structure are additional parameters controlling the gross photosynthesis at the stand level (e.g. Stenberg et al., 1994, 1995; Palmroth and Hari, 2001; Sigurdsson, 2001; Mäkelä et al., 2006). Nevertheless, the photosynthesis processes are quite well understood and the large amount of studies utilizing the eddy covariance technique to study these processes at ecosystem level have shown that most of the uncertainty regarding controlling factors and processes are located in the soil (Schulze, 2006).

Net ecosystem productivity has now been studied in the Northern part of Europe during a decade or more (Lindroth et al., 1998; Markkanen et al., 2001; Pilegaard et al., 2002; Suni et al. 2003) and in the Nordic countries, annual balances have been quantified at more than 10 forest sites. The aim of this paper is to try to address the question of which factors control the gross primary productivity and the ecosystem respiration of Nordic forests of different species growing in different climates. We also wish to analyse the differences (if any) between the forests and seek to find some common biogeophysical factors, which can explain these differences.

2. Material and methods

2.1. Site description

This study comprises eight different forests, deciduous as well as conifers, growing in different climates in Sweden, Denmark, Finland and Iceland (Table 1). The climate spans from temperate to subarctic with a mean annual temperature range between −0.5 and 8 °C and precipitation range of 300–900 mm (Table 1). The sites are part of the Nordic centre for studies of interaction between ecosystems and climate, NECC (www.necc.nu). All sites are equipped with eddy covariance systems for measurement of fluxes of CO_2 between forest and atmosphere.

2.2. Determination of leaf area index

2.2.1. Sorø. In Sorø leaf area index (LAI) was measured using the LAI-2000 (Li-Cor Inc., Lincoln, USA) on four 200 m transects extending outwards from the flux tower. Measurements were done with 15 m intervals at nine different occasions during the growing season 2002. The maximum value of 5 occurred in beginning of August. Details about the measurements and the calculations are given by Pilegaard et al. (2003).

2.2.2. Norunda and Skyttorp. In Norunda and Skyttorp LAI was measured with the LAI-2000 on fixed positions located on three transects in Norunda and two in Skyttorp. The number of sampling points were fifty in Norunda and thirty in Skyttorp. Measurements were done once per month during the growing season of 2004 and the LAI was averaged for the whole season and for all sampling points. The measurements were corrected for leaf clumping by multiplying with a factor of 1.65 according to the manufacturers recommendations (LAI-2000 Instruction Manual; Li-Cor Inc., Lincoln, USA)

2.2.3. Hyytiälä. Breast height diameter and height of all trees within 75 sample plots in eight directions (from azimuth angle 0 with 45° angle) were measured within 180 m radial distance from the base of the flux tower. Each one of the circular sample plots had an area of 100 m^2. A locally determined allometric relationship between stem dimensions and leaf biomass and area was then used to estimate leaf area per tree. The leaf area index was calculated as a weighted average considering the variation in sampling density.

2.2.4. Flakaliden. Leaf area index was measured on 26 August 2002 using the LAI-2000. Total number of sampling points were one hundred equally distributed on four ca. 300 m long transects. Correction for leaf clumping was made using a correction factor of 1.65 according to the manufacturers recommendations (LAI-2000 Instruction Manual; Li-Cor Inc., Lincoln, USA).

2.2.5. Sodankylä. The needle area was determined by applying a regression model to tree data from 859 trees from 41 sample

Table 1. Site characteristics. Air temperature and precipitation are 30 years averages

Site name Lat Long	Temp Precip.	Climate	Species Dominant/subdomin.	Ground vegetation	LAI	Age (yr)	Soil type
Norunda 60.1 N 17.5 E	5.5 527	Hemiboreal	*Pinus sylvestris/Picea abies*	*V. myrtillus; Vaccinium vitis-idaea;* mosses	4.5	99	Sandy podzolic glacial till
Skyttorp 60.1 N 17.6 E	5.5 527	Hemiboreal	*Pinus sylvestris/Picea abies*	*V. myrtillus; Vaccinium vitis-idaea;* mosses	3.8	35	Sandy podzolic glacial till
Flakaliden 64.1 N 19.5 E	1.2 523	Boreal	*Picea abies*	*Vaccinium vitis-idaea; V. myrtillus;* mosses	3.4	30	Sandy podzolic glacial till
Abisko 68.4 N 19.05 E	−0.9 305	Subarctic	*Betula pubescens ssp.*	*Empetrum hermophroditum; Vaccinium vitis- idaea; V. myrtillus;* mosses	2.6[a]	Un-even	Podzol
Hyytiälä 61.8 N 24.4 E	3.0 700	Boreal	*Pinus sylvestris*	*Calluna vulgaris; Vaccinium vitis-idaea; V. myrtillus;* mosses, lichens	3.3	39	Haplic podzol
Soroe 55.5 N 11.63 E	8.3 730	Temperate	*Fagus silvatica*	*Anemone nemorosa; Mercurialis perennis*; grasses	5.0	84	Mollisol
Sodankylä 67.22 N 26.38 E	−1.0 499	Boreal	*Pinus sylvestris*	*Calluna vulgaris*; *Vaccinium vitis-idaea;* Lichens; mosses	1.7[a]	100	Haplic podzol
Vallanes 65.3 N 14.9 W	3.4 738	Maritime subarctic	*Larix sibirica*	*Betual nana; Vaccinium uliginosum;* grasses	1.8[a]	13	Andosol

[a]For sites with tree layer LAI < 3, the LAI of the ground vegetation was added.

Table 2. Specifications of the different flux system installations with reference to relevant publications where instrumentation and site specific characteristics are described in more detail

Site	References and comments
Norunda	Grelle et al. (1999)
Skyttorp	Same system as in Grelle et al. (1999) with following deviations: Gill R3, measurement height 15 m, maximum tree height 12 m, fetch ca 250 m all wind directions
Flakaliden	Wallin et al. (2001), Berggren et al. (2004)
Abisko	Johansson (2006)
Hyytiälä	Markkanen et al. (2001)
Soroe	Pilegaard et al. (2003)
Sodankylä	Aurela (2005)
Vallanes	Bjarnadottir and Sigurdsson (2007)

plots which were located in eight equally separated (45°) directions around the flux tower. Tree data were recorded every 50 m distance from the mast. The regression model between the breast height diameter and the needle area was based on destructive sampling (trunks, branches, whorls) of 10 trees of representative sizes. Needle areas were determined from the dry masses after measuring needle dry masses and lengths of subsamples and applying a second order polynomial to relate needle length and area. The tree layer LAI of each sample plot was estimated by first calculating leaf area for each tree according to the diameter in the sample plots, then summing leaf area for the whole sample plot and dividing by sample plot area. The average tree layer LAI of the whole forest was then taken as the average of the sample plot LAI values. The LAI of the ground vegetation was estimated on basis of degree of coverage by the vascular plant communities (Table 1). It was assumed that the leaf area of the vascular plants completely covered the ground, that is, unity LAI per area covered by vascular plants. The total LAI was then estimated as the sum of tree and ground vegetation LAI.

2.2.6. Abisko. The leaf area of the tree layer was measured monthly over several seasons using the LAI-2000 on five transects with ca. 50 sampling points. The maximum value occurred in the shift July/August. The leaf area of the ground vegetation was estimated from leaf mass estimates of the dominant ground vegetation species and on specific leaf area measurements made earlier in an adjacent experiment in the same type of forest and with similar ground vegetation as were the flux tower was located. Maximum leaf area index was calculated as the sum of tree layer and ground vegetation leaf areas per unit of ground area.

2.2.7. Vallanes. The leaf area index of the forest canopy and the forest floor vegetation was measured three times during the growing season with the LAI-2000. Measurements were made during overcast days with sensor heads always facing north using a 180° lens cap. Measurements were made along eight 50 m long transects around the flux tower on ca. 200 sampling points including both ground vegetation and tree layer. The average of all values were taken as the LAI of the forest.

2.3. Flux measurements

The net ecosystem exchange of CO_2 is measured by the eddy covariance method at all sites following the so called 'Euroflux methodology' (Aubinet et al., 2000) comprising a Gill ultrasonic anemometer (R2 or R3; Solent, U.K.) an infrared closed-path gas analyser (Li-6262, Li-Cor Inc, Lincoln, USA) except for Vallanes where an open-path gas analyser is used (LI-7500; Li-Cor Inc., Lincoln, USA) instead of the closed-path and in Sodankylä where a Metek USA-1 ultrasonic anemometer (Metek GmbH, Hamburg, Germany) is used for wind speed measurements and a LI-7000 (Li-Cor Inc., Lincoln, USA) closed path gas analyser is used for CO_2 concentration. The flux data from the Vallanes system was calculated using the so-called WPL correction (Webb et al., 1980) and corrections were also made for the additional heat transfer caused by the heat dissipation from the gas analyser body using the empirical relationship deduced by Burba et al. (2006). References to publications where details about quality control of data and on the different site specific set ups are given in Table 2.

Climatic measurements were made in the same towers as was used for flux measurements. For this study the following standard parameters were measured; air temperature and humidity in ventilated radiation shields, photosynthetic active radiation (PAR) using quantum sensors (LI-190; Li-Cor., Inc., Lincoln, USA), and soil moisture using different type of sensors. In Vallanes, soil water potential was measured instead of water content.

2.4. Data analysis

The analysis in this paper was based on half-hourly fluxes and climatic variables measured under well-mixed conditions separated into two data sets: one daytime data set and one nighttime data set, respectively. Only data where $u^* > 0.3$ ms^{-1} were selected for both day and night and all data was checked for quality. Data representing a normal year without exceptional weather events were chosen by the respective site managers at sites were several years of data were available. The daytime data were analysed in

the following way:

(1) The data were split into half-monthly periods (from 1st to 15th; from 16th to end of the month).

(2) The measured net flux was fitted to the following equation:

$$F_c = -(F_{csat} + R_d)\left[1 - \exp\left(\frac{-\alpha\ \mathrm{PAR}}{F_{csat} + R_d}\right)\right] + R_d. \quad (1)$$

The dark respiration (R_d), saturation flux (F_{csat}) and quantum efficiency (α) parameters and their uncertainties (standard error) were estimated for each half-monthly period.

(3) The mean air temperature, PAR, vapour pressure deficit and soil moisture were calculated for the corresponding periods.

Mean nighttime fluxes and air temperatures were calculated for the corresponding half-monthly periods including wintertime when data were available and data was fitted to the Lloyd and Taylor (1994) equation:

$$\mathrm{NEE}_{night} = R_{10} \cdot e^{308.56 \cdot \left(\frac{1}{56.02} - \frac{1}{T - 227.13}\right)}, \quad (2)$$

where R_{10} is the respiration at 10 °C and T is temperature. This equation is theoretically based but with coefficients optimised to give best fit to an extensive data set on soil respiration (Lloyd and Taylor, 1994). We choose here to use the same coefficients as was found by Lloyd and Taylor leaving only the R_{10} as a fitting parameter.

3. Results

3.1. Nighttime ecosystem respiration

The mean half-monthly nighttime NEE (ecosystem respiration) showed a strong seasonal variation with similar pattern for all sites (Fig. 1). Lowest values occurred in the winter with typical minimum rates of 0.3–0.5 μmol m^{-2} s^{-1} for the coldest sites while the highest wintertime rates occurred for the warmest site, Soroe with 1.8–2.0 μmol m^{-2} s^{-1}. The low rates were relatively constant from late December to March, after which it started to increase in the southernmost site. The highest growing season rates occurred for Soroe in the second half of June with

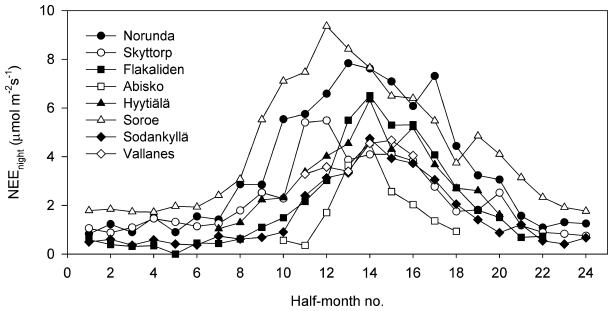

Fig. 1. Mean half-monthly nighttime respiration rates for $u* > 0.3$ m s^{-1} for the respective sites.

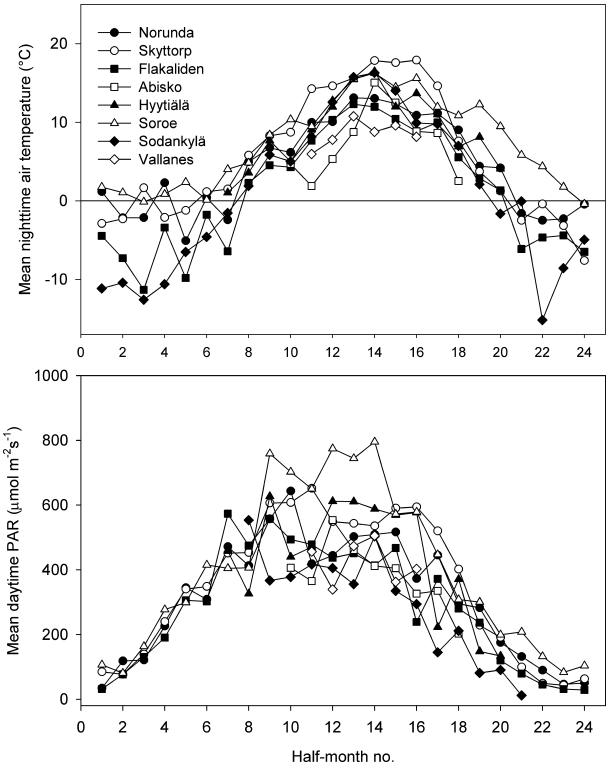

Fig. 2. Mean half-monthly nighttime air temperature (top) and mean half-monthly daytime photosynthetic active radiation (bottom) at the different sites.

9.3 μmol m^{-2} s^{-1} while the maxima occurred typically one month later in the other sites. The difference between the highest and the lowest rates across sites varied from an order of magnitude in winter to a factor of two in the heart of the growing season.

The seasonal variation of nighttime NEE is largely a reflection of some effective temperature of the ecosystem, here represented by air temperature, which show the same seasonal pattern (Fig. 2) as the ecosystem respiration. Plotting the mean half-monthly respiration rates against the corresponding nighttime air temperature showed the expected exponential increase with increasing temperature (Fig. 3). The fit to the Lloyd and Taylor (1994) equation was generally quite good with r^2 in the range 0.671–0.968 (Table 3). The parameter R_{10}, that is, the total ecosystem respiration at 10 °C ranged between 2.485 ± 0.300 μmol m^{-2} s^{-1} for Abisko and 5.752 ± 0.179 μmol m^{-2} s^{-1} for Norunda. A plot of nighttime NEE normalized with the fitted R_{10} for the respective sites showed a good fit with $r^2 = 0.969$ for all sites taken together (Fig. 4). The plot of residuals against temperature (Fig. 4) also showed that there was little systematic bias. It was only for temperatures below zero that there was a small tendency that the model (eq. 2) overestimated the respiration. The r^2 for modelled nighttime NEE versus measured for absolute values for all sites taken together was slightly lower, 0.864, but still quite good (Fig. 5).

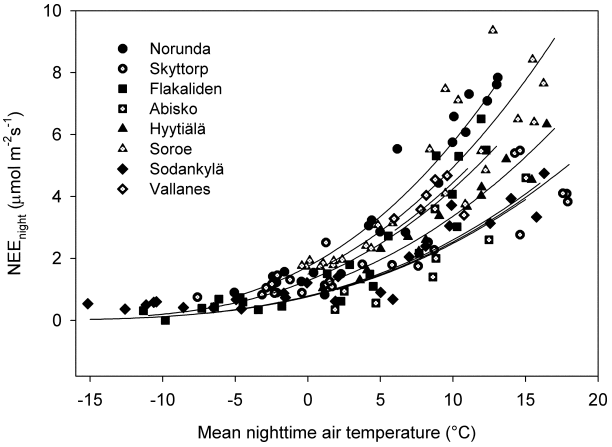

Fig. 3. Mean half-monthly nighttime NEE for $u^* > 0.3$ m s^{-1}. The fitted curves are according Lloyd and Taylor (1994) using their original parameters except the respiration rate at 10 °C which was fitted separately for each site.

3.2. Daytime NEE responses to environmental variables

All parameters of the light response curve showed a strong seasonal variation (Fig. 6). It was most pronounced for F_{csat} and R_d, which had a maximum in the middle of the summer. The variation was less pronounced for α, which showed a steady increase over the season. The errors became larger at the end of the season due to low light levels (cf. Fig. 2). Soroe showed a slightly different behaviour than the other forest particularly when concerning F_{csat} with a pronounced maximum in the first half of June, then a decrease followed by an increase to a secondary maximum in the second half of September. Thereafter the F_{csat} dropped rapidly to very low values. The light use efficiency parameter behaved in a similar fashion but here both maxima occur about two weeks earlier (Fig. 6). The variations in these parameters were more smoothly at the other sites with a single maximum value in the middle of the summer.

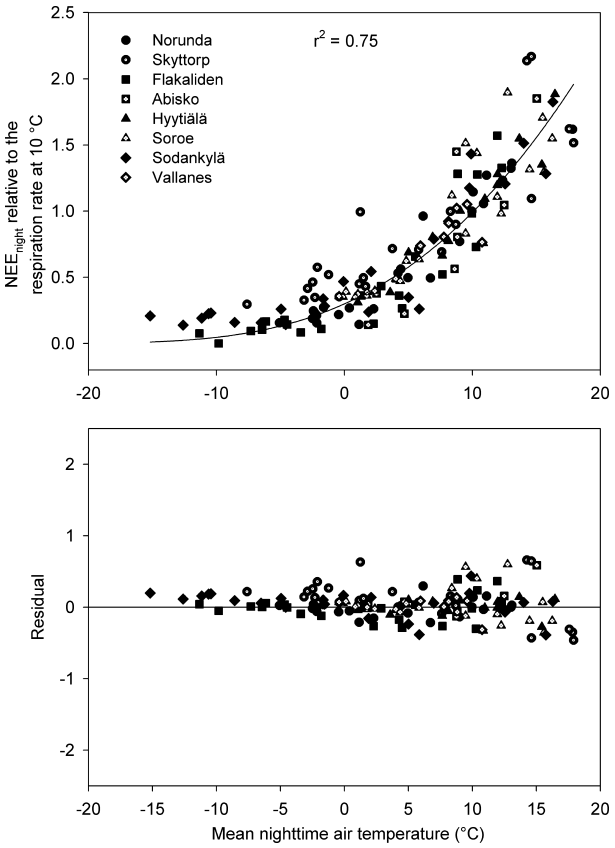

Fig. 4. Modelled mean half-monthly ecosystem respiration, normalized by the fitted respiration at 10 °C (top) and residual between modelled and measured relative respiration versus mean half-monthly nighttime air temperature.

The correlation between the fitted parameters of eq. (1) and the environmental variables; air temperature, photosynthetic photon flux density, vapour pressure deficit and soil moisture are shown in Tables 4(a–h). The regressions were estimated for the period of

Table 3. Result of the fitting of mean nighttime fluxes to the Lloyd and Taylor (1994) equation: *SE* = standard error of the fit, R_{10} = the fitted parameter corresponding to the respiration at 10 °C and *SD* R_{10} = the standard deviation of the parameter.

Site	r^2	*SE* (µmol m^{-2} s^{-1})	R_{10} (µmol m^{-2} s^{-1})	*SD* R_{10} (µmol m^{-2} s^{-1})
Norunda	0.9672	0.6447	5.7517	0.1787
Skyttorp	0.6714	0.8318	2.5288	0.1774
Flakaliden	0.9251	0.7675	4.2451	0.2531
Abisko	0.7196	0.7995	2.485	0.3006
Hyytiälä	0.9677	0.3881	3.3597	0.0986
Soroe	0.8793	1.1894	4.9367	0.2512
Sodankylä	0.9289	0.5057	2.5988	0.1349
Vallanes	0.9420[a]	0.2011	4.8788	0.1082

[a]One outlayer removed; soil moisture was extremely high during this period resulting in strongly reduced respiration.

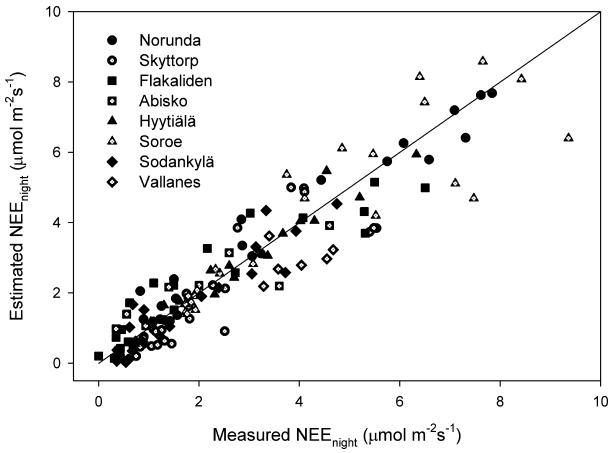

Fig. 5. Estimated ecosystem respiration rate versus measured ecosystem respiration for the different sites. The only parameter that was fitted was the respiration rate at 10 °C according Lloyd and Taylor (1994) equation. The line show is the 1:1 line.

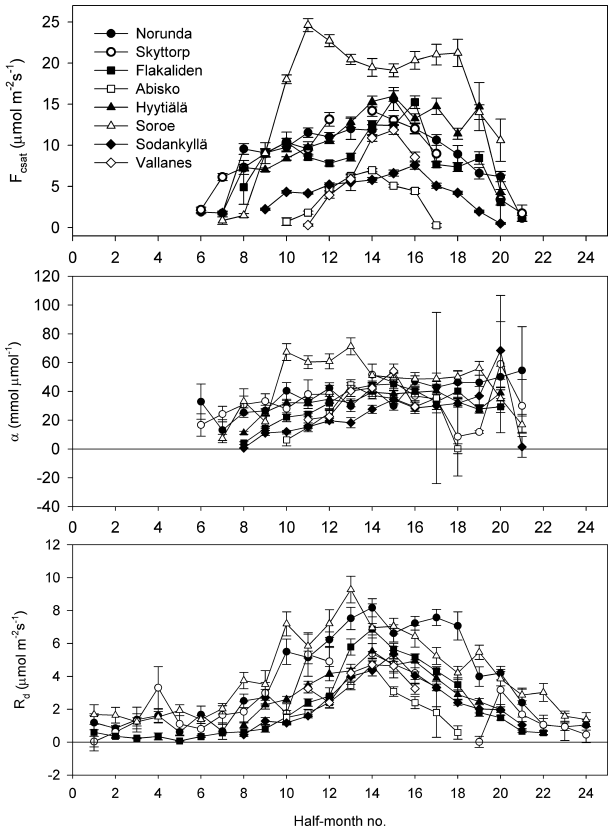

Fig. 6. Seasonal variation of the parameter values and their respective standard errors for F_{csat} (top), α (middle) and R_d (bottom) at the different sites.

the year when the mean half-monthly daytime air temperatures were positive. All sites showed relatively strong correlation between the three light response parameters particularly between F_{csat} and R_d and between α and R_d; the determination coefficient r^2 ranged between 0.393 (Flakaliden) and 0.803 (Abisko) for F_{csat} and R_d, and between 0.312 (Sodankylä) and 0.850 (Skyttorp) for α and R_d. The situation was different for the correlation between F_{csat} and α where, for example, Norunda and Sodankylä showed no correlation while for instance r^2 was 0.717 for Vallanes and 0.876 for Skyttorp.

Of the environmental variables, air temperature showed the highest correlation with F_{csat} and R_d at all sites except Flakaliden and Vallanes where the correlation was strongest to soil moisture. The situation was different for the light use efficiency parameter; the correlation was generally quite weak to all environmental variables except for Skyttorp where there was a strong correlation to all variables (Table 4) of which air temperature showed the highest $r^2 = 0.825$. All sites showed strong correlation between the environmental variables particularly between PAR and vapour pressure deficit. Hyytiälä showed strong negative correlation between soil moisture and respectively F_{csat}, R_d and α bearing in mind that there was also strong negative correlation between air temperature and soil moisture. Interestingly, Vallanes showed similar strong negative correlation to soil moisture for these parameters without having a very strong correlation between temperature and soil moisture (Table 4).

3.3. Gross photosynthesis

The light response curve was fitted to the measured net ecosystem exchange during daytime meaning that it is affected by both photosynthesis and respiration. By adjusting the curve so that it passes through the origin, it represents the gross photosynthesis of the whole ecosystem, and thus, the sum of F_{csat} and R_d represent the maximum gross photosynthesis under non-limiting light conditions. According to the biochemistry of C3 photosynthesis (e.g. Farquhar and von Caemmerer, 1982) both rubisco activity and electron transport, key elements controlling maximum rates of photosynthesis, are temperature limited and plotting $F_{csat} + R_d$ against air temperature could reveal if there are such temperature limitations in the forests studied here. There was, however, no clear picture emerging from such plots (Fig. 7). For some sites, the relationship was quite linear, for example, for Norunda, Skyttorp, Abisko and Sodankylä, while the relationship to temperature was more complex at the other sites. Another factor influencing this relationship is the canopy development and Soroe, which is a deciduous forest, showed a more complex behaviour, which also indicated that there was a temperature limitation. Flakaliden, Hyytiälä, Sodankylä and Vallanes had lower maximum capacity in spring than in autumn for the same temperature. Mäkelä et al. (2004) shows that there was substantial variation in the leaf specific photosynthetic capacity during the growing season that was linked to temperature with a delay. As they applied this to the Hyytiälä eddy covariance derived GPP values, it explained major proportion of the observed inter annual variation (Mäkelä et al., 2006).

The mean summertime gross photosynthetic capacity showed a large variation between the sites (Fig. 8) with a three-fold

Table 4. Correlation between the parameters of the light response curve and environmental variables for the different sites. Up arrow indicate positive and down arrow negative correlation while minus sign indicate indifferent correlation

Norunda

	F_{csat}	α	R_d	T_a	PAR	VPD	SWC
F_{csat}	1						
α	0.054 -	1					
R_d	0.618 ↑	0.349 ↑	1				
T_a	0.892 ↑	0.075 -	0.769 ↑	1			
PAR	0.177 ↑	0.206 ↓	0. 028 -	0.212 ↑	1		
VPD	0.402 ↑	0.015 -	0. 227 ↑	0.473 ↑	0.795 ↑	1	
SWC	0.413 ↓	0.005 -	0.172 ↓	0.379 ↓	0.508 ↓	0.484 ↓	1

Skyttorp

	F_{csat}	α	R_d	T_a	PAR	VPD	SWC
F_{csat}	1						
α	0.876 ↑	1					
R_d	0.712 ↑	0.850 ↑	1				
T_a	0.863 ↑	0.825 ↑	0.795 ↑	1			
PAR	0.631 ↑	0.628 ↑	0.625 ↑	0.637 ↑	1		
VPD	0.702 ↑	0.694 ↑	0.726 ↑	0.942 ↑	0.671 ↑	1	
SWC	0.128 ↓	0.309 ↓	0.350 ↓	0.160 ↓	0.015 -	0.183 ↓	1

Flakaliden

	F_{csat}	α	R_d	T_a	PAR	VPD	SWC
F_{csat}	1						
α	0.265 ↑	1					
R_d	0.393 ↑	0.778 ↑	1				
T_a	0.310 ↑	0.340 ↑	0. 632 ↑	1			
PAR	0.039 -	0.105 ↓	0.001 -	0.216 ↑	1		
VPD	0.002 -	0.100 ↓	0.009 -	0.244 ↑	0.741 ↑	1	
SWC	0.420 ↑	0.051 -	0.067 -	0.149 ↑	0.042 -	0.081 -	1

Abisko

	F_{csat}	α	R_d	T_a	PAR	VPD	SWC
F_{csat}	1						
α	0.415 ↑	1					
R_d	0.803 ↑	0.645 ↑	1				
T_a	0.770 ↑	0.775 ↑	0.886 ↑	1			
PAR	0.187 ↑	0.227 ↑	0.295 ↑	0.332 ↑	1		
VPD	0.477 ↑	0.354 ↑	0.460 ↑	0.558 ↑	0.793 ↑	1	
SWC	–	–	–	–	–	–	1

difference between one group of sites (Abisko, Sodankylä and Vallanes) having the lowest capacity and Soroe which had the highest capacity. Intermediate capacity had Norunda, Skyttorp, Hyytiälä and Flakaliden.

Table 4. cont'd

Hyytiälä

	F_{csat}	α	R_d	T_a	PAR	VPD	SWC
F_{csat}	1						
α	0.176 ↑	1					
R_d	0.555 ↑	0.528 ↑	1				
T_a	0.478 ↑	0.193 ↑	0.829 ↑	1			
PAR	0.040 -	0.012 -	0.341 ↑	0.543 ↑	1		
VPD	0.054 -	0.051 -	0.340 ↑	0.668 ↑	0.846 ↑	1	
SWC	0.541 ↓	0.509 ↓	0.757 ↓	0.511 ↓	0.143 ↓	0.134 ↓	1

Soroe

	F_{csat}	α	R_d	T_a	PAR	VPD	SWC
F_{csat}	1						
α	0.548 ↑	1					
R_d	0.627 ↑	0.694 ↑	1				
T_a	0.676 ↑	0.353 ↑	0.725 ↑	1			
PAR	0.365 ↑	0.146 ↑	0.493 ↑	0.481 ↑	1		
VPD	0.192 ↑	0.053 -	0.362 ↑	0.477 ↑	0.850 ↑	1	
SWC	0.281 ↓	0.129 ↓	0.452 ↓	0.641 ↓	0.221 ↓	0.306 ↓	1

Sodankylä

	F_{csat}	α	R_d	T_a	PAR	VPD	SWC
F_{csat}	1						
α	0.049 -	1					
R_d	0.625 ↑	0.312 ↑	1				
T_a	0.534 ↑	0.003 -	0.639 ↑	1			
PAR	0.104 ↑	0.368 ↓	0.011 -	0.312 ↑	1		
VPD	0.098 -	0.138 ↓	0.088 -	0.531 ↑	0.830 ↑	1	
SWC	0.196 ↓	0.301 ↓	0.279 ↓	0.216 ↓	0.047 -	0.002 -	1

Vallanes

	F_{csat}	α	R_d	T_a	PAR	VPD	SWC
F_{csat}	1						
α	0.717 ↑	1					
R_d	0.494 ↑	0.792 ↑	1				
T_a	0.339 ↑	0.406 ↑	0.340 ↑	1			
PAR	0.000 -	0.008 -	0.261 ↑	0.104 ↑	1		
VPD	0.085 -	0.001 -	0.027 -	0.161 ↑	0.320 ↑	1	
SWC	0.421 ↓	0.627 ↓	0.939 ↓	0.311 ↓	0.393 ↓	0.011 -	1

3.4. Site intercomparison

In order to analyse the difference between sites, the mean parameter values during the heart of the growing season, that is, June to August, were calculated. The mean parameter values plus the gross photosynthesis at roughly maximum photon flux density, set to 1200 μmol m^{-2} s^{-1}, were estimated from the mean light

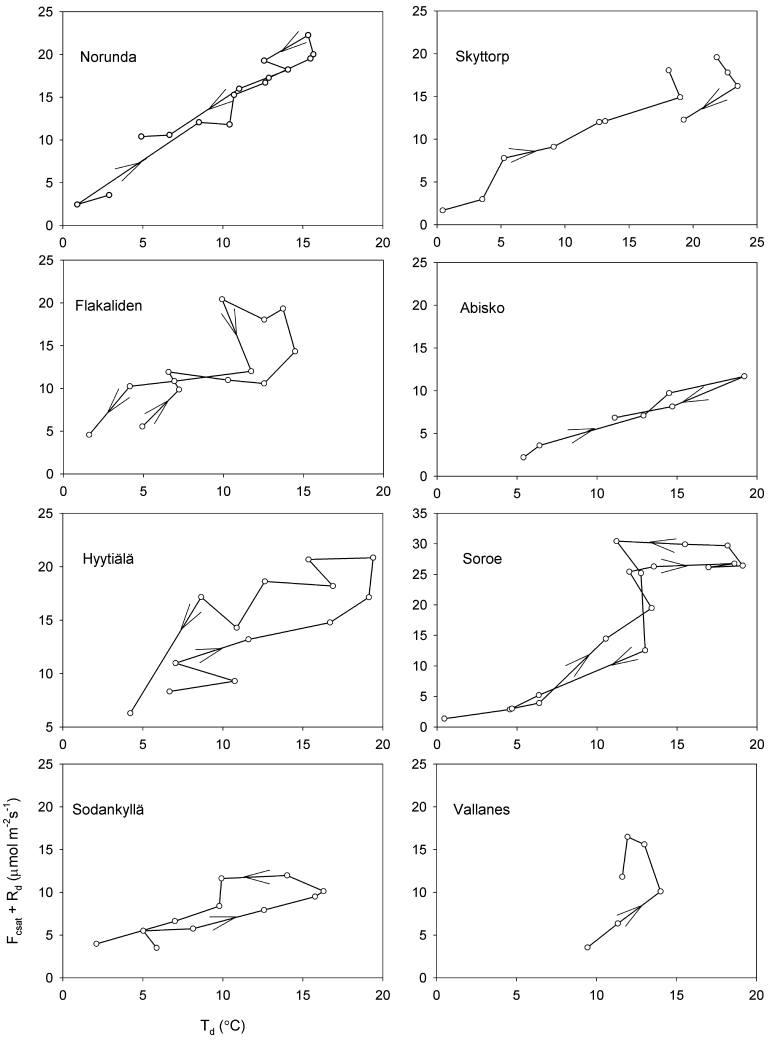

Fig. 7. F_{csat} versus mean half-monthly daytime air temperature at the different sites. The arrows shows the temporal development with arrow pointing in direction of increasing time.

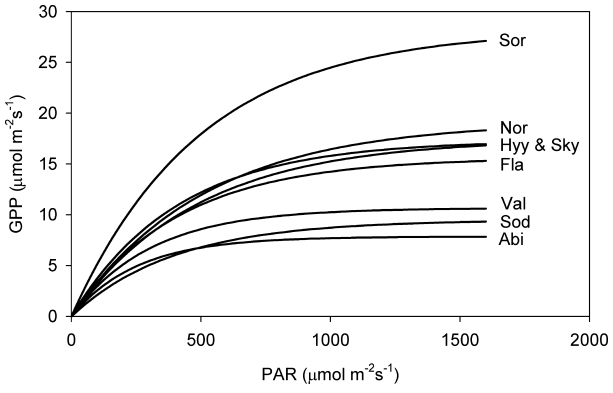

Fig. 8. GPP versus PAR during the core of the growing season, that is, June to August for which period the parameters of the respective light response curves were averaged. The GPP value at PAR = 1200 μmol m^{-2}s^{-1} were taken as maximum GPP for the respective site.

response curves and were then correlated to the following stand properties: mean summertime air temperature, leaf area index, canopy mass turnover rate, stand age, leaf longevity and species. It turned out that leaf area index was the parameter that best explained the difference between the sites (Fig. 9) which maybe not was so unexpected when considering photosynthesis parameters, but more interesting was that leaf area index also explained the difference in respiration between the sites through the parameter R_d. When normalizing the R_d with the LAI-dependent function, the only remaining correlation was to age (Fig. 10).

4. Discussion

Wintertime respiration rates in Flakaliden and Sodankylä were comparable to those reported for three boreal forests in Canada with similar mean annual temperature, the Southern Old Aspen, Southern Old Black Spruce and Southern Old Jack Pine, respectively (Griffis et al., 2003). The Canadian stands had mean daily maximum rates (November to March) in the range 0.7–1.4 g C m^{-2}d^{-1}, which is close to the range 0.73–1.2 μmol m^{-2}s^{-1} found here for maximum half-monthly means for Flakaliden and Sodankylä for the corresponding period. The maximum rates in the middle of the growing season were similar

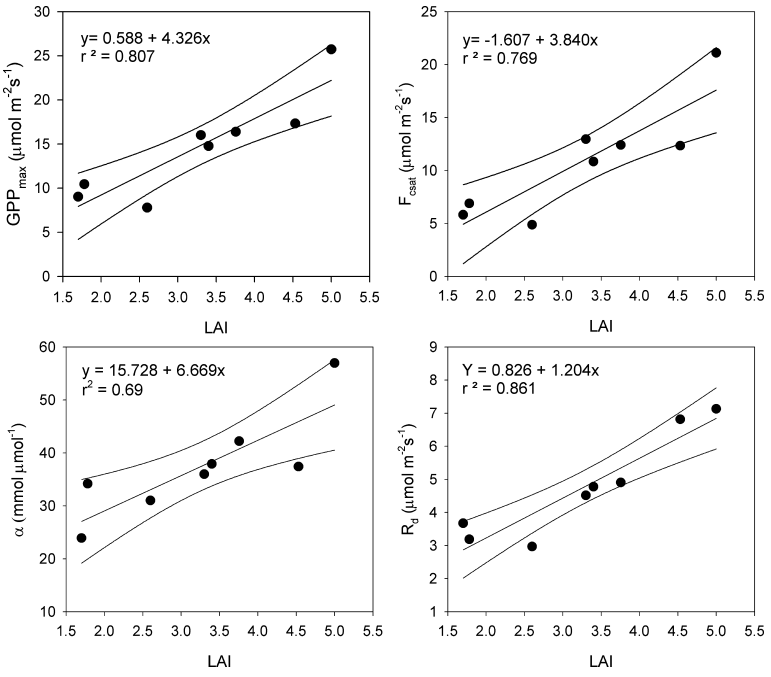

Fig. 9. Seasonal mean values (June–August) of the respective light response curve parameters and for maximum GPP plotted against the LAI for the different sites.

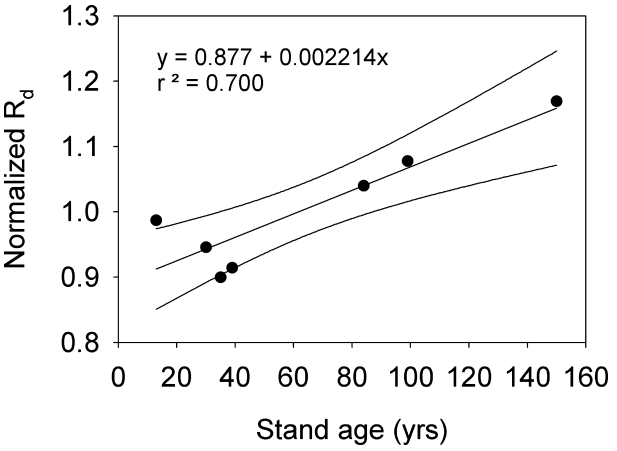

Fig. 10. Normalized R_d plotted against stand age. Here the Abisko site is not included since it is a natural forest.

as well. However, the numbers are not directly comparable since they represent different averaging periods, daily means for the Canadian stands and two-weekly means for the stands reported here.

The beech forest at Soroe has previously been compared with a beech forest in France (Granier et al., 2002) showing stunning similarity in fluxes, both for components and for the net ecosystem exchange. The two stands showed unusually similarity in dynamics over the whole year despite the large geographic distance between them.

Data on CO_2 exchange in larch stands are scarce but Wang et al. (2004) reported a whole year of data from a Japanese larch forest located in Hokkaido and found ecosystem respiration rates of ca. 3.7 μmol $m^{-2}s^{-1}$ at an air temperature of 10 °C which is lower than the 4.5 μmol $m^{-2}s^{-1}$ found here for Vallanes at the corresponding temperature. It is possible that part of this excess is caused by the so-called Burba correction (Burba et al., 2006) which is not suited for the windy conditions at the Icelandic site.

It is interesting to note that the Norunda site, which is a source to the atmosphere (e.g. Lindroth et al., 1998) because of unusually high annual respiration, does not deviate very much from the other forests of this study. The respiration rate in Norunda is lower than that of Soroe during most of the season; it is only in the autumn when Norunda shows the highest rates (Fig. 1). Such enhanced respiration rates have also been reported for other forests, for instance, a Russian taiga spruce stand, where historical disturbances was the cause of the high respiration rates (Milyukova et al., 2002) causing also this forest to become a source to the atmosphere. However, the ecosystem respiration of the forests studied here are comparable to values of corresponding forest in other regions but with similar climates.

It was expected that temperature should have a very strong control over ecosystem respiration but it was surprising that the Lloyd and Taylor (1994) model fitted so well for all the different forests with only one free parameter, the respiration rate at 10 °C. In the original paper by Lloyd and Taylor (1994), only soil respiration (including ground vegetation) was analysed and data were estimated from chamber measurements. Such measurements often give tighter relationships to temperature than does the whole ecosystem respiration since the temperature, usually a soil temperature quite close to the soil surface, is more strongly connected to the measured local flux. It is much more

difficult to find a single temperature which is representative for the whole ecosystem respiration. Our data showed smaller relative residuals (Fig. 4) as compared to those of Fig. 3. In Lloyd and Taylor (1994) but that is probably because we are using mean values spanning much longer time periods than those of Lloyd and Taylor. With the approach used here, the temperature sensitivity becomes the same for all sites but it is not constant over the temperature range. It increased from 2.59 at −10 °C to 0.71 at 20 °C, in line with many other studies showing that Q_{10} indeed is higher at low temperatures (e.g. Raich and Schlesinger, 1992; Kirschbaum, 1995; Tjoelker et al., 2001; Davidson and Janssens, 2006). This also implies that this model is better to use for extrapolations beyond the temperature regime for which its parameter is determined as compared to a traditional Q_{10} based type of exponential model where overestimation at high temperatures is a problem. Considering the complexity of soil respiration with the soil being a 'veritable soup' of thousands of different organic C-compounds (so well put by Davidson and Janssens, 2006) and considering that our sites represent a range of tree species, ground vegetation, soil types etc., it was quite unexpected that the same coefficients of the Lloyd and Taylor (1994) equation would give such good results.

The parameters of the light response curve, representing the photosynthesis of the stands, showed similar seasonal dynamics except for Soroe where two maximum values occurred, one early and the other late in the season. Similarly, the α parameter also had two maximum values but both occurred in the early part of the season. The reason for this behaviour at Soroe is probably that the ground vegetation consisting of *Anemone nemorosa, Mercurialis perennis* and some grasses develop vigorously in spring before the bud break of the beech trees (Pilegaard et al., 2002). When the canopy starts to close, the ground vegetation declines and eventually disappears since light levels become very low on the forest floor. Soroe also had an R_d distribution which was skewed towards the early part of the season coinciding with the peaks in F_{csat} and α. This might as well be a reflection of autotrophic respiration from the ground vegetation. The other sites showed more similarity in the seasonal patterns with a single maximum although the absolute values were different. The maximum values were reached practically at the same time for all parameters, namely during the second half of July (Fig. 6). This maximum co-inside quite well with the maximum in air temperature (Fig. 2) but it is later than the maximum in incoming light.

The strong cross correlation between practically all environmental variables makes it hard to reveal which of the variables that are in control. This is an effect of the strong seasonality in all variables including the ones related to the CO_2 exchange. The only possible way to handle this problem, when analysing in situ data like this, is to work with much larger data sets. For some of the sites studied here, there are multiple-years of data and Lagergren et al. (this issue) have made such an analysis for the sites Norunda, Soroe and Hyytiälä.

The finding that LAI best explained the differences between sites for both photosynthesis and respiration parameters are quite interesting. The strong coupling between productivity and respiration has been shown previously (e.g. Valentini et al., 2000; Janssens et al., 2001) but it has not been shown that all of the parameters controlling the net ecosystem productivity for the different forests (i.e. the parameters of the light response curve) are so tightly controlled by the LAI. The reason for this behaviour can be understood when considering the functioning of a forest ecosystem. The vegetation is feeding a great deal of the carbon fixed by the photosynthesis to the roots and into the soil as root exudates. Recently a series of interesting experiments in both pine and spruce forests in northern Sweden have shown a strong linkage between canopy photosynthesis and root respiration (Högberg et al., 2005; Olsson, 2006). These studies have shown that as much as 60% of the soil respiration from the forest floor originates from canopy assimilation, which is a function of LAI. Total ecosystem respiration is, thus heavily dependent on root respiration and on the prompt microbial decomposition of exudates and root litter (e.g. Ryan and Law, 2005). Then there is a large stock of slowly decaying carbon that contributes very little to the ecosystem respiration. The observed relationship between LAI, photosynthesis and respiration suits well to this scheme.

The existence of a relationship between LAI and tree productivity has been demonstrated earlier in many studies (e.g. Pereira, 1994) and it relate to the fact that canopy photosynthesis is strongly controlled by light absorption (e.g. Monteith, 1977), which in turn is largely determined by the LAI under similar radiation conditions. Other factors such as water and nitrogen availability does also affect photosynthesis both directly through effects on stomatal aperture and Rubisco activity and indirectly, in the long-term, through effects on leaf area. Since none of the stands showed any sign of water or nutrient stress during the years investigated, it is not surprising that the parameters of the light response curve that relate to canopy photosynthesis show a strong relationship to LAI of the respective forests. It was more of a surprise that also the variations of the parameter determining the dark respiration of the stands were largely explained by LAI. These results are in accordance with Reichstein et al. (2003) who found that peak leaf area index was a good predictor of standardized soil respiration in global analysis covering 17 different forests.

The LAI was measured by different methods in the different stands and this creates some uncertainty regarding the comparability between stands when it concerns this parameter. LAI is time demanding and laborious to measure with destructive methods and no matter how it is measured it is always hampered by scaling uncertainties. In Norunda and Skyttorp LAI was measured both with the optical methods and with the indirect methods based on allometry related to tree dimensions. The different methods gave similar results, which indicate that the methodological differences maybe are not so important.

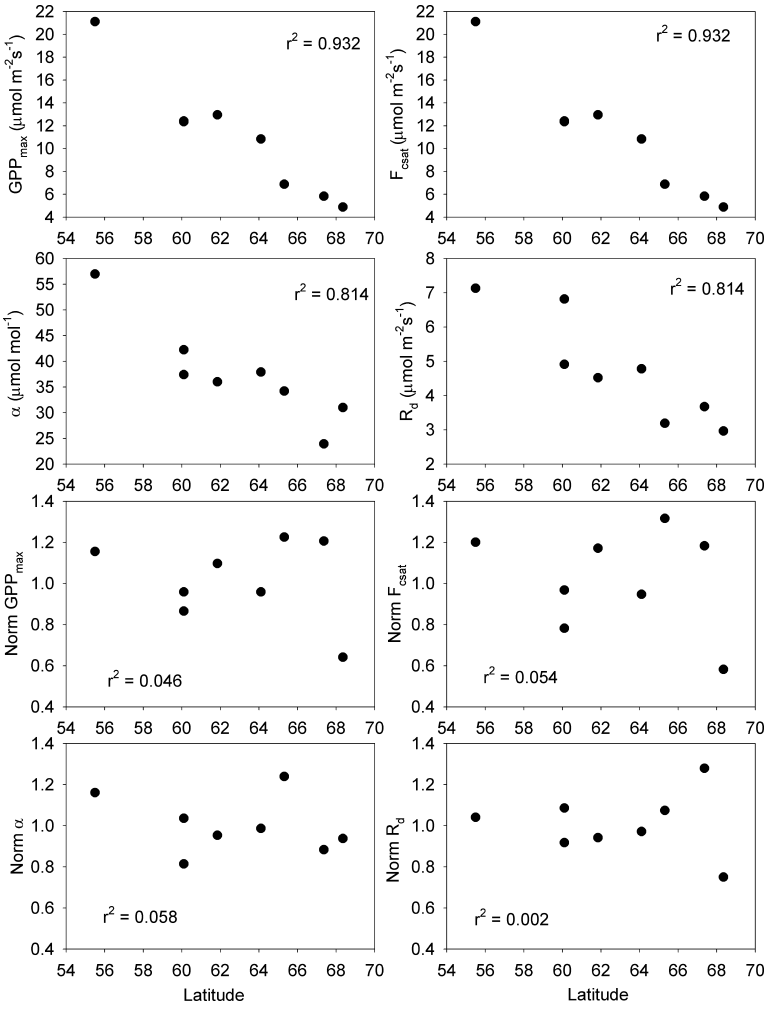

Fig. 11. Four upper panels: Seasonal mean values (June–August) of the respective parameters of the light response curve plotted against latitude of the different sites. Four lower panels: The same values as in the upper panels but parameters normalized by the LAI-relationship for the respective parameters (see Fig. 9).

Without doing a detailed error analysis, which is outside of the scope of this investigation, we estimate the uncertainty in the LAI values to about 0.5 across all sites. Adding this uncertainty to the LAI values does not change the results concerning the shown relationships to LAI for both photosynthesis and respiration parameters.

When we tried to explain the variation between the sites, we tested also latitude as a dependent variable and the correlation was even higher for this parameter (Fig. 11) as compared with the LAI. We do not consider latitude to be a relevant parameter in this context but is interesting because previously reported data on NEE for European forests showed the best correlation with latitude (Valentini et al., 2000) without being able to explain why this relationship existed. When we plotted our data normalized for LAI, the latitudinal dependency disappeared completely (Fig. 11). Thus, it cannot be excluded that the relationship found by Valentini et al. (2000) was in fact a relationship to LAI but it is, on the other hand not conclusive, since we only show that the component (respiration and photosynthesis) parameters correlate strongly with LAI and this does not necessarily mean that the NEE does.

We believe that our results open new possibilities for remote sensing methods to be used also to estimate respiration. The main drivers for gross photosynthesis and respiration, that is, temperature and photon flux densities, can both be estimated from satellites (e.g. Wan et al., 2004; Olofsson and Eklundh, 2006). In addition, leaf area index, can also be estimated from satellites (e.g. Eklundh et al., 2003) and, thus, all the necessary parameters can in principle be derived solely from satellite measurements. There are of course other factors than LAI that affect stand respiration, that is, site history, management practices etc but we still believe that the possibility to estimate the net ecosystem productivity from satellite data, maybe in combination with other type of data such as land-use/history, has taken a step forward. It should, however, also be pointed out that we have not analysed the relationship between photosynthesis and respiration parameters over the course of a whole year; here we have only analysed the relationships during summer.

5. Conclusions

(1) Total ecosystem respiration for the type of forests studied here can be well estimated by the Lloyd and Taylor equation if the mean respiration rate at 10 °C is known.

(2) Leaf area index largely explains differences in photosynthetic as well as in respiration characteristics between the sites.

(3) The dark respiration normalized for LAI is weakly dependent on stand age.

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