

Measurement of net ecosystem exchange, productivity and respiration in three spruce forests in Sweden shows unexpectedly large soil carbon losses

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Abstract Measurement of net ecosystem exchange was made using the eddy covariance method above three forests along a north-south climatic gradient in Sweden: Flakaliden in the north, Knottåsen in central and Asa in south Sweden. Data were obtained for 2 years at Flakaliden and Knottåsen and for one year at Asa. The net fluxes (N_{ep}) were separated into their main components, total ecosystem respiration (R_t) and gross primary productivity (P_g). The maximum half-hourly net uptake during the heart of the growing season was highest in the southernmost site with $-0.787 \text{ mg CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ followed by Knottåsen with $-0.631 \text{ mg CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ and Flakaliden with $-0.429 \text{ mg CO}_2 \text{ m}^{-2} \text{ s}^{-1}$. The maximum respiration rates during the summer were highest in Knottåsen with $0.245 \text{ mg CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ while it was similar at

the two other sites with $0.183 \text{ mg CO}_2 \text{ m}^{-2} \text{ s}^{-1}$. The annual N_{ep} ranged between uptake of $-304 \text{ g C m}^{-2} \text{ year}^{-1}$ (Asa) and emission of $84 \text{ g C m}^{-2} \text{ year}^{-1}$ (Knottåsen). The annual R_t and P_g ranged between 793 to $1253 \text{ g C m}^{-2} \text{ year}^{-1}$ and -875 to $-1317 \text{ g C m}^{-2} \text{ year}^{-1}$, respectively. Biomass increment measurements in the footprint area of the towers in combination with the measured net ecosystem productivity were used to estimate the changes in soil carbon and it was found that the soils were losing on average $96\text{--}125 \text{ g C m}^{-2} \text{ year}^{-1}$. The most plausible explanation for these losses was that the studied years were much warmer than normal causing larger respiratory losses. The comparison of net primary productivity and P_g showed that ca 60% of P_g was utilized for autotrophic respiration.

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Introduction

Forests store vast amounts of carbon both above and below-ground (e.g., Dixon 1994) and they constitute an important sink for atmospheric CO_2 on a global scale (IPCC 2001). The net gain of carbon (N_{ep}) is determined by the balance between two large components, the gross uptake by photosynthesis (P_g) and the total ecosystem respiration (R_t). A small shift in

one of these components can have large impact on the uptake of CO_2 from the atmosphere. Concern has been raised that future global warming will lead to losses of soil carbon which would diminish the sink and provide positive feedback to the climate. However, temperature, moisture and nutrient availability are all factors which influence both productivity and decomposition and the way changes in climate will influence N_{ep} is not straightforward. Janssens et al. (2001), for instance, show that productivity exerts stronger control over respiration than does temperature. In a comprehensive analysis of the future impact of climate change on European ecosystems, Schröter et al. (2005) arrive at the conclusion that during the coming century forest growth will increase more than decomposition but at the end of the century the decomposition rate becomes higher and the carbon sink diminishes.

Rates of both decomposition and plant production are related to climatic factors but also to disturbance (e.g., Chapin et al. 2002). The building up of carbon pools is a slow process, manifested through the small positive difference between production and respiration over most of the life cycle of a forest, while disturbance can release large amounts over short time (Körner 2003). An example of man-made disturbance is the harvesting of forests when the forest turns from a sink to a source (Kowalski et al. 2004) but the disturbance effect is relatively short-lived and after a relatively short period of time, the forest acts as a sink again. In Northern Europe practically all forests are managed and management has probably had a positive effect on the above-ground stock which is increasing in many countries (Liski et al. 2002). It is more uncertain what effect management has on the soil carbon stock. Peltoniemi et al. (2004) found that soil carbon in the humus layer decreased up to 20 years after harvest and then increased again for upland forests in southern Finland. They concluded that soil carbon increased when integrated over the whole rotation period. Olsson et al. (1996) showed that the carbon pool in the organic layer had decreased strongly 15–16 years after clear-felling for sites in southern and northern Sweden. Soil history and management practices together with climate apparently play an important role in how the soil pools are affected.

In this study, which is part of the LUSTRA project (Olsson, [this volume](#)), we have investigated the

relationship between net ecosystem exchange, productivity and decomposition in three forests of similar species and age in Sweden along a climatic gradient from the north to the south. We measured the N_{ep} by eddy covariance during two years and separated the net flux into P_{g} and R_{t} . The net primary productivity, P_{n} , was determined from biomass measurements within the footprint area of the flux towers, and foliage litterfall and fine root turnover from measurements in nearby plots. We could thus also assess the relationship between P_{g} and P_{n} , which according to some hypotheses should be a conservative measurement (Waring et al. 1998) and we could also estimate the changes in soil carbon pools as a residual between N_{ep} and total biomass increment.

Material and methods

Site description

The three sites in this study are located along a climatic gradient in Sweden from the north to the south with a difference in mean annual air temperature (30-year average) of 4.3°C and in annual precipitation of 105 mm with the coldest and driest in the north and warmest and wettest in the south. The difference in climate is also manifested in a difference in length of growing season, which on average increases from 120 days in the north to 190 in the south (threshold of 5°C). The stands are of the same species and approximately of the same age growing on podzolic soils (Table 1). The moisture class was dry to mesic at Knottåsen and Flakaliden and moist at Åsa.

Flux and climatic measurements

The same type of closed path eddy covariance flux systems (In Situ Flux Systems AB, Ockelbo, Sweden) were used at all three sites with only minor differences between sites. Sonic anemometer (Gill R3 (Åsa and Knottåsen), Gill R2 (Flakaliden; Solent, UK) was used for wind speed measurement and an infrared gas analyzer (LI-6262, Li-Cor Inc., Lincoln, USA) for CO_2 and H_2O concentration measurements. The air was sucked at a rate of ca 8 l min⁻¹ with a 6 m long, 4 mm inner diameter polyethylene tubing using a membrane pump down to the gas analyser

Table 1 Site characteristics for the LUSTRA sites. The data on tree biomass refer to the year 2002

	Asa	Knottåsen	Flakaliden
Latitude, Longitude	57°08' N, 14°45' E	61°00' N, 16°13' E	64°07' N, 19°27' E
Altitude (m a.s.l.)	190 m	320 m	320 m
Major Tree species ^a	<i>Picea abies</i>	<i>Picea abies</i>	<i>Picea abies</i>
Ground vegetation type ^a	No veg.	<i>Vacc. myrtill.</i>	<i>Vacc. myrtill.</i>
Soil type according FAO (1990) ^a	Gley Podzol	Podzol	Podzol
Projected leaf area index	3.7	2.5	3.4
Site class index (tree height at 100 years) ^a	31	23	17
Stand age in 2002 ^a	39	39	43
Tree density (no. ha ⁻¹)	2834	3463	2603
Maximum tree height (m)	25.1	16.5	12.7
Basal area (m ² ha ⁻¹)	32.3	14.7	20.7
Stem biomass (g C m ⁻²)	4360	1174	1600
Foliage biomass (g C m ⁻²)	569	393	529
Live branch biomass (g C m ⁻²)	1690	944	1330
Dead branch biomass (g C m ⁻²)	114	39	54
Stump biomass (g C m ⁻²)	503	164	232
Coarse root (>5 cm diam.) biomass (g C m ⁻²)	824	206	289
Fine root (<5 cm diam.) biomass (g C m ⁻²)	394	204	279
Field layer biomass (g DS m ⁻²) ^a	9	158	91
Bottom layer biomass (g DS m ⁻²) ^a	56	279	250
Organic layer carbon content (g C m ⁻²) ^a	12600	1270	870
Mineral soil carbon (0–100 cm) (g C m ⁻²) ^a	10400	4590	6350

^a From Berggren et al. (2004)

which was placed in a temperature-controlled system box. Sonics were heated to provide data under hoar frost conditions as well. Data collection and analyses were made in real time by Ecoflux software. Mains power was available at all sites. Pure nitrogen was used to purge the reference cell of the gas analyzer at a low rate. The gas analyzer was calibrated for CO₂ by means of an automatic 2-point calibration system in Asa and Knottåsen using technical air of known CO₂ concentration and N₂ for span and zero estimations. The system in Flakaliden was calibrated manually. Calibration was done on a bi-weekly basis in the automatic system and at about monthly intervals with manual calibration. The flux system data analysis was made according to the Euroflux methodology (Grelle and Lindroth 1996; Aubinet et al. 2000) using planar fit for estimation of vertical wind component. The flux systems were placed ca 3 m above the highest trees at all sites. Fetch conditions were generally quite good within the nearest 200–300 m from the towers and footprint

analysis showed that the main part of the flux came from within a radius of ca 100 m during daylight hours. The energy balance closure estimated from the annual sum of the fluxes were on average 89% for Flakaliden, 92% for Knottåsen and 78% for Asa.

Climatic measurements were made in the same towers as were used for flux measurements. Standard parameters were measured i.e., air and soil temperature, air humidity, solar and net radiation, photosynthetic active radiation (PAR), soil heat flux, soil moisture etc. Details about instrumentation and installations are given by Berggren et al. (2004). Gaps in climatic data were taken from nearby stations within 10 km from the flux sites. The absorbed PAR was estimated as the difference between incoming and reflected PAR.

Flux data analysis

In this analysis, data were available for 2001 and 2002 in Flakaliden and Knottåsen and for 2002 in

Asa. The first steps in the data analysis was careful selection of the data when the flux measurement systems worked properly and to remove spikes, which could not be attributed to morning flushes. The removal of spikes was done manually and based on experience from this type of measurement. The rate of change of CO₂ storage in the air below the flux measurement level was then added to all remaining flux data to obtain the biotic flux. It was assumed that the measured concentration of the flux system was representative for the whole stand when calculating the storage flux. The gap filling was then done according the following:

1. Data for $u^* > \text{threshold}$ both at night and during the day were selected. The threshold value was determined by plotting nighttime flux plus storage, normalised by the temperature, against u^* and then it was judged by eye where the normalized flux plus storage started to decrease with u^* . The threshold was found to be 0.3 m s^{-1} in Flakaliden and Knottåsen and 0.25 m s^{-1} in Asa.
2. Grouping of the half hourly data by half-monthly periods. If <5 days at the beginning and end of the month, these days were included in closest period.
3. Fitting

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

for each period and where F_c is the 30-min daytime biotic flux and PAR is the photosynthetic active radiation. F_{csat} , R_d and α are fitting parameters.

4. Fitting

$$F_c = R_0 \cdot \exp(k \cdot T) \quad (2)$$

for each period and where F_c is the nighttime biotic flux, R_0 and k are fitting parameters and T is the air temperature.

5. In case no relationship with temperature could be obtained for nighttime data, the mean value during the night for the whole period was used instead.
6. For longer periods, mean diurnal half hourly look-up tables were created with all existing data with at least 10 values per half hour available.

Half-hourly values of P_g were estimated by applying the relationship between nighttime flux and temperature (for $u^* > \text{threshold}$) during daytime and subtracting the measured net flux. In case model relationship could not be established, the mean nighttime respiration was used during daytime. P_g was set to zero during the night. Values for longer periods of time were estimated by summation of the gap filled components.

The gaps in the latent heat fluxes were filled by fitting a Penman–Monteith type of model (Monteith 1965) to the measured data. The surface conductance in the P–M model was estimated on the basis of the so-called Lohammar equation using vapour pressure deficit and global radiation as drivers (e.g., Lindroth 1985). The fitting was made for periods of different length, typically a month long and centred at the periods where data was missing.

The uncertainty in the estimated annual N_{ep} was estimated in the following way:

1. The uncertainty caused by gap filling was estimated by randomly removing a certain number of values, filling them according to the method used, and then comparing the estimated gap filled values with the ‘true’ measured values. This procedure was repeated several times, and a mean gap filling error was estimated for each site and year. The lengths of the respective gaps were taken into account when the gap filling errors were scaled to the full year.
2. The possible systematic errors due to, e.g., drift in the instruments were assumed to be 5% for the CO₂ fluxes following Grelle (1997) who analysed errors on a measurement system similar to the ones used in this study.
3. The total error in the annual sums where calculated as the sum of the respective errors mentioned above.

Biomass measurements

Standing biomass and growth were estimated within a 100 m radius of the flux-towers. 16 circular plots with a radius of 7 m were spread evenly around each tower in the autumn 2005. Diameter was measured on all trees, and height, height growth over the last five years and annual ring width for the last six years (measured on bore cores) was measured on sample

trees. The number of sample trees was 68, 45 and 69 in Asa, Knottåsen and Flakaliden, respectively. By empirical functions of height growth and annual ring widths, height and diameter was assessed on all tallied trees for the last six years. Dry weight biomass for different fractions of the trees was estimated with biomass functions by Marklund (1988) and the carbon content was assumed to be 50% of the biomass in all fractions (Thörnqvist 1985). Mean carbon sequestration per year was estimated by the mean difference in the estimated carbon content in living biomass between two consecutive years between 1999 and 2005. In this analysis, only data for 2001 and 2002 were used. The error in biomass increment was estimated on the basis of the error in the regression equations used, the estimated error in the measurements of the annual ring widths and on the variance between the sample plots.

The leaf area index was estimated from measurements with the gap frequency method using a Plant Canopy Analyzer (LI-2000, Li-Cor Inc., Lincoln, Nebraska, USA) with corrections made for leaf clumping. The litterfall and fine root turnover were measured in nearby plots and details are given in Berggren Kleja et al. (this volume).

Results

Weather

The 30-years (1961–1990) mean annual temperature was 1.2, 3.4 and 5.5°C in Flakaliden, Knottåsen and Asa respectively and the corresponding mean annual precipitation was 523, 613 and 688 mm (Berggren et al. 2004) respectively. All sites and years were

warmer than normal and particularly Flakaliden which was 2.7°C above normal and Asa with 2.0°C above normal, both in 2002 (Table 2). Mean annual precipitation was much higher than normal in Flakaliden in 2001, while it was about 10% below normal in 2002. Knottåsen had near normal precipitation in 2001 and about 13% lower in 2002, while Asa had near normal precipitation in 2002.

The growing season (5°C threshold) was shortest in Flakaliden with 153 and 154 days for 2001 and 2002, respectively. The corresponding values for Knottåsen were 174 and 158 days and for Asa, the length was 192 days (in 2002) (Table 2).

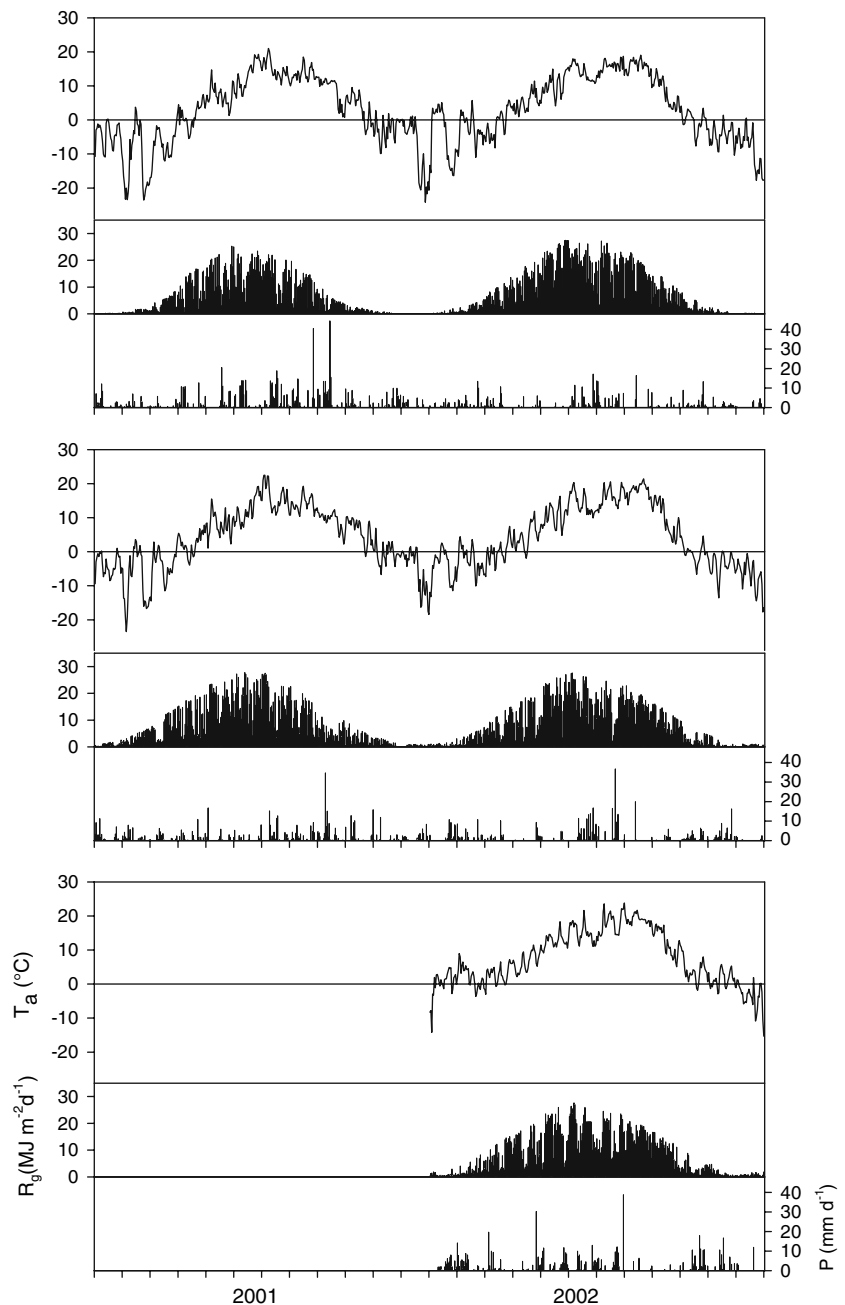
The mean daily maximum and minimum temperatures were relatively similar for all years and all sites; Flakaliden had 21.0°C and 19.1°C as maximum temperature in 2001 and 2002, Knottåsen slightly higher with 22.5°C and 21.4°C for the corresponding years while Asa reached 23.8°C in 2002 (Fig. 1). The corresponding minimum temperature was −24.2°C and −17.7°C for Flakaliden, −23.5°C and −17.7°C for Knottåsen and −15.3°C for Asa, respectively. It is noticeable that Flakaliden had an almost month-long period of warm weather in January 2002. This period was warm at the other sites as well but actually warmest in the northernmost site, Flakaliden (Fig. 1). It is also interesting to notice that the daily pattern in weather conditions is quite similar at all sites which was also reflected in the carbon exchange patterns (cf. below). This similarity also goes for the daily mean radiation, which reaches similar values at all sites in the middle of the summer because of the longer day-length at the higher latitudes. The annually accumulated radiation amounts were also quite similar with 3173–3328 MJ year^{−1} except for Flakaliden in 2001 when the rainy weather decreased the annual amount to 2335 MJ year^{−1}.

Table 2 Mean annual temperature, annual precipitation and evaporation and start/stop/length of growing season at the three sites

Site	Year	Mean air temp (°C)	Annual precip. (mm)	Annual evap. (mm)	Start date (dd/mm)	Stop date (dd/mm)	Length (days)
Flakaliden	2001	2.3	857	168	28/4	26/9	153
	2002	3.9	458	187	19/4	18/9	154
Knottåsen	2001	3.8	588	264	27/4	17/10	174
	2002	4.5	533	349	19/4	24/9	158
Asa	2002	7.5	712	198	28/3	5/10	192

The start/stop of the growing season is defined as the time when the mean daily air temperature is higher/lower than 5°C three days in a row

Fig. 1 Mean daily air temperature, daily short-wave radiation and precipitation for the years 2001 and 2002 in Flakaliden (top) and Knottåsen (middle) and for 2002 in Asa (bottom)

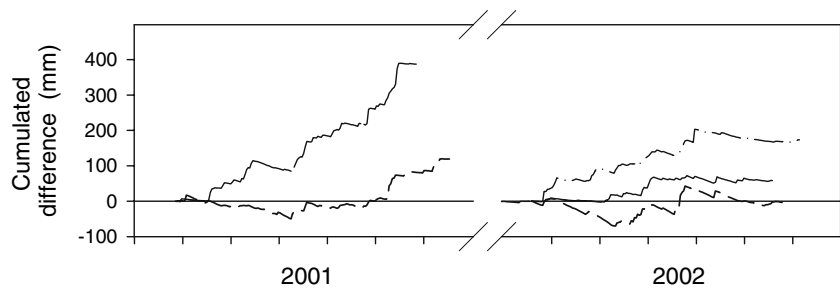


The precipitation exceeded evaporation at all sites and all years on an annual basis but the conditions during the growing season were different. Flakaliden had a surplus of water during both growing seasons (Fig. 2) but Knottåsen showed a deficit of maximum -50 mm in the first half of July 2001 and -70 mm in the first half of June 2002. Asa had a surplus of water during the whole growing season 2002 (Fig. 1).

Net ecosystem productivity

The period when most of the net uptake occurs is generally shifted slightly towards the earlier part of the growing season (cf. Fig. 4 below) because respiration rates are low while radiation is already at high levels. The period May–August can be defined as the ‘main uptake season’ and in order to

Fig. 2 Cumulated difference between precipitation and evaporation during the growing seasons ($T > 5^{\circ}\text{C}$) in Flakaliden (solid), Knottåsen (dashed) and Asa (dash-dot), respectively



characterize all three sites, year 2002 when data from all sites were available, was chosen for comparison of half-hourly values. The mean N_{ep} was highest in Asa with $-0.217 \text{ mg CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ and lowest in Flakaliden with $-0.066 \text{ mg CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ and with Knottåsen in between with $-0.128 \text{ mg CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ (Table 3). The median values were consistently higher at all sites indicating a skewness in the distributions. The maximum uptake rates (5% percentile) showed similar patterns between the sites with the highest rates in Asa (Table 3). The maximum effluxes (95% percentile) on the other hand were similar in Flakaliden and Asa with $0.183 \text{ mg CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ and highest in Knottåsen with $0.245 \text{ mg CO}_2 \text{ m}^{-2} \text{ s}^{-1}$. Thus, in spite of being the warmest site, Asa did not show the highest efflux rates. However, it should be pointed out that there were more missing data at Asa during this period than at the two other sites.

The differences found in the half-hourly N_{ep} rates are also reflected in the mean daily rates with Asa showing the highest and Flakaliden the lowest mean daily values (Fig. 3). The difference in respiration is also clearly visible especially in the winter when Knottåsen shows the highest losses. The cumulated fluxes show that Flakaliden was a sink both years

with a range of -122 to $-86 \text{ g C m}^{-2} \text{ year}^{-1}$, Knottåsen was a source in 2001 with and a small sink in 2002 which gave a range of -22 to $+88 \text{ g C m}^{-2} \text{ year}^{-1}$ while Asa showed the largest annual uptake with -315 to $-287 \text{ g C m}^{-2} \text{ year}^{-1}$ in 2002 (Fig. 3; Table 4). The ranges given here include the errors estimated for the annual values (Table 4) while only the mean values are shown in Fig. 3.

Component fluxes

The N_{ep} separated into its main components; P_g and R_t are shown in Fig. 4. The general seasonal pattern is similar for all sites except that the variability in both R_t and P_g are larger in Flakaliden than at the other sites. The P_g curve is more symmetric with the maximum occurring in June/July while R_t tends to stay high longer into the later part of summer. It is also clear from the seasonal pattern of P_g that the growing season as defined by significant P_g ($>10\%$ of max P_g) is longer in the south than in the north. In Asa we actually have significant P_g already in February while the corresponding uptake starts about one month later in Knottåsen and Flakaliden. It should be noted that the traditional definition of growing season based on temperature threshold (Table 2) is much shorter than the period of significant P_g .

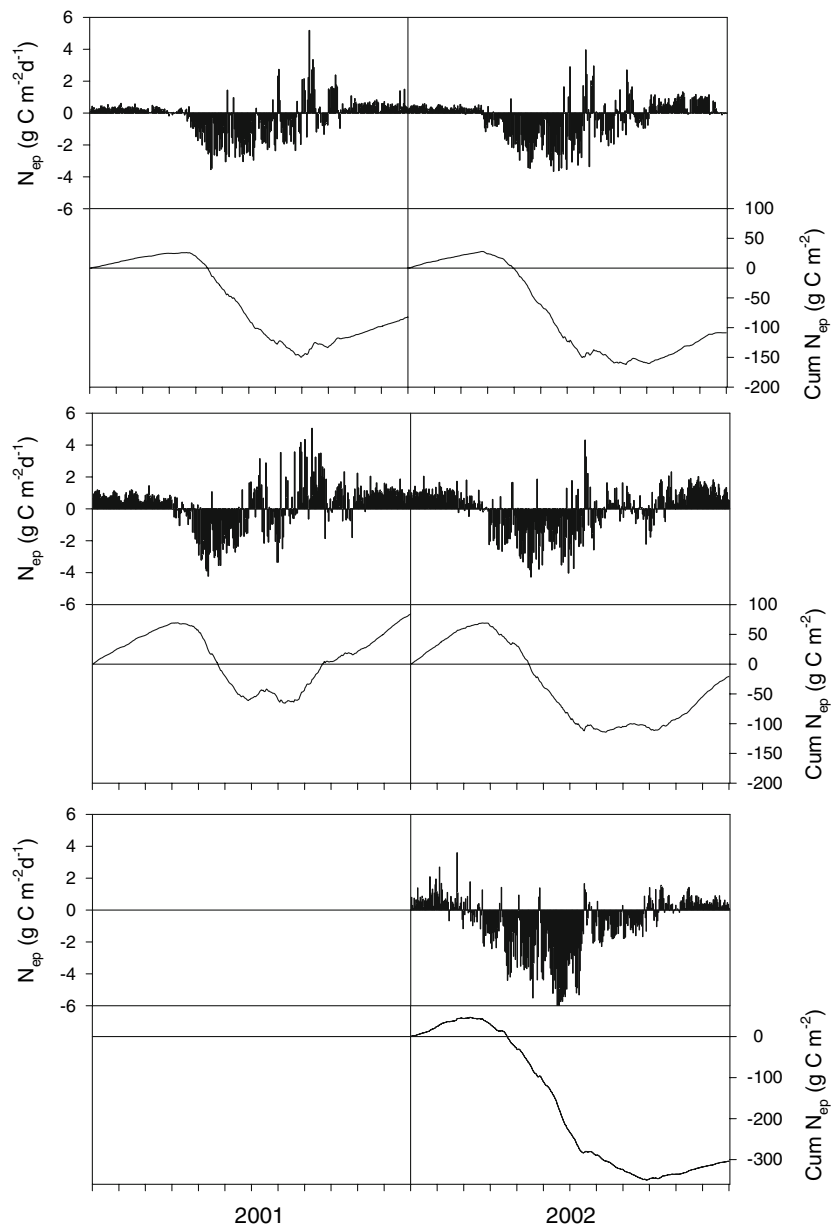
Plotting weekly mean values of R_t against the corresponding mean weekly air temperature shows the very strong control of temperature on respiration (Fig. 5). The northernmost site, Flakaliden, showed the highest temperature sensitivity with almost twice as high sensitivity to temperature as did Knottåsen and Asa, which, on the other hand were quite similar (Fig. 5). The base respiration was lowest in Flakaliden, highest in Knottåsen and intermediate in Asa. The light use efficiency expressed as slope of the regression line between incident PAR and gross

Table 3 Flux statistics for N_{ep} based on the half-hourly values in 2002 at the three sites

Statistic	Flakaliden	Knottåsen	Asa
95% percentile	0.183	0.245	0.183
5% percentile	-0.429	-0.631	-0.787
Median	-0.096	-0.173	-0.267
Mean	-0.066	-0.128	-0.217
N	4510	3535	1713

Data are from the main uptake season, defined here as May–August and units are $\text{mg CO}_2 \text{ m}^{-2} \text{ s}^{-1}$

Fig. 3 Daily sums of net ecosystem exchange (N_{ep}) and annually cumulated N_{ep} for 2001 and 2002 in Flakaliden (top) and Knottåsen (middle) and for 2002 in Asa (bottom), respectively



primary productivity for weekly values was quite similar for all three sites (Fig. 6). The relationship at this timescale was quite linear and did not show any tendency of saturation at high PAR values.

The mean monthly N_{ep} in 2001 (Fig. 7) shows that Flakaliden has negative values from April to August while Knottåsen has negative values only during three months, April–July. During 2002 Flakaliden and Knottåsen are more similar but the wintertime N_{ep} is almost twice as high (positive) in Knottåsen as

compared to Flakaliden. Asa shows high wintertime N_{ep} in January–February, almost as high values as for Knottåsen but in November–December Asa is similar to Flakaliden and much lower than Knottåsen. In Asa, negative N_{ep} occurred during seven months, March–September, which makes a big difference compared to the other two sites.

The total ecosystem respiration is highest in July in Flakaliden and Knottåsen in 2001 with almost as high values in August (Fig. 7). In summer 2002,

Table 4 Productivity and respiration at the three LUSTRA field sites

Site	Year	P_g	R_t	N_{ep}		P_{TL}	P_{RL}	P_B	P_n	Δ_{soil}		P_B/P_g	P_n/P_g
				L	H					L	H		
Flakaliden	2001	−875	793	−86	−94	92 ^a	98 ^a	182 ± 9	372	−105	−79	0.21	0.43
	2002	−1136	1027	−111	−122	92 ^a	98 ^a	195 ± 9	385	−93	−64	0.17	0.39
Knottåsen	2001	−1169	1253	88	75	101 ^a	132 ^a	143 ± 7	376	−238	−211	0.12	0.32
	2002	−1237	1216	−16	−22	101 ^a	132 ^a	152 ± 7	385	−143	−123	0.12	0.31
Asa	2002	−1317	1013	−287	−315	118 ^a	101 ^a	325 ± 9	544	−47	−1	0.25	0.41

P_g = Gross primary productivity, R_t = Ecosystem respiration, N_{ep} = Net ecosystem productivity, P_{TL} = Total above ground litter productivity, P_{RL} = Root litter productivity, P_B = Biomass productivity, P_n = Net primary productivity and Δ_{soil} = Change in soil carbon content ($= -1 * N_{ep} - P_B$). All parameters expressed as $g\ C\ m^{-2}\ year^{-1}$. 'L' and 'H' refer to the range when including the high and low error estimates respectively in the flux measurements. The ratios P_B/P_g and P_n/P_g has been multiplied by -1 in order to have positive values

^a Measured or estimated on nearby plot similar to the flux plot (Berggren Kleja et al., [this volume](#))

Flakaliden has the highest R_t followed by Knottåsen and Asa with the lowest mean monthly rates. The summertime R_t in Flakaliden was much lower in 2001 as compared to 2002 while the situation was the opposite in Knottåsen. The mean monthly P_g was slightly higher in Knottåsen as compared to Flakaliden in 2001 while all three sites were quite similar in 2002 with the difference mainly being the length of the uptake season.

Productivity and respiration

The biomass increment estimated from tree rings and empirical functions shows that Asa has clearly the highest growth with $325 \pm 9\ g\ C\ m^{-2}\ year^{-1}$ in 2002 followed by Flakaliden with 182 ± 9 and $195 \pm 9\ g\ C\ m^{-2}\ year^{-1}$ in 2001 and 2002, respectively and that Knottåsen had the lowest growth rate with 143 ± 7 and $152 \pm 7\ g\ C\ m^{-2}\ year^{-1}$ in 2001 and 2002 (Table 4). The estimated net primary productivity (P_n) which includes estimated tree litter fall and fine root litter showed smaller difference between Flakaliden and Knottåsen with 372–385 $g\ C\ m^{-2}\ year^{-1}$ while Asa had 544 $g\ C\ m^{-2}\ year^{-1}$ in P_n . The ratio (multiplied by -1) between annual biomass increment and P_g varied between 0.12 and 0.25 and the ratio between P_n and P_g varied between 0.31 and 0.43 (Table 4).

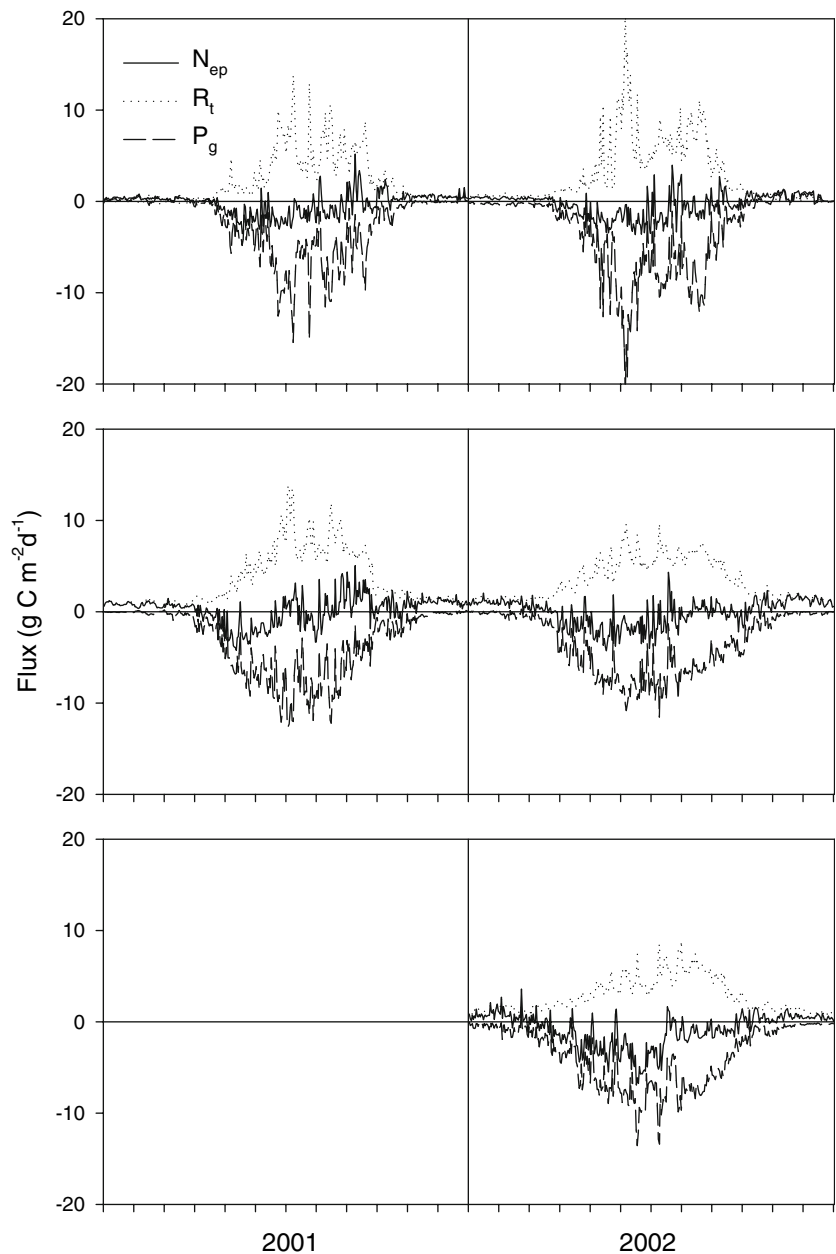
The rate of change in soil carbon was estimated as the difference between the annual biomass increment and the net ecosystem productivity ($N_{ep} * -1$). All sites showed that the soil was losing carbon every year (Table 4). The largest loss was estimated for

Knottåsen in 2001 with -238 to $-211\ g\ C\ m^{-2}\ year^{-1}$ and the smallest for Asa with -47 to $-1\ g\ C\ m^{-2}\ year^{-1}$. The ranges given include the estimated errors in biomass increment and N_{ep} , respectively.

Discussion

The seasonal pattern of net ecosystem productivity is similar to other boreal forests in Scandinavia. Markkanen et al. (2001) reported maximum uptake rates in the end of June being typically $-0.53\ mg\ CO_2\ m^{-2}\ s^{-1}$ in a pine forest in Finland (Hyytiälä; 61°51' N) of about the same age as the forests studied here. This value is intermediate between Flakaliden and Knottåsen (Table 3) while Asa shows higher maximum uptake rates. Zha et al. (2004) measured CO_2 exchange in a slightly older (50 years) pine stand located at in Huhus (62°52' N) in Finland and in this forest the maximum uptake rates were similar to those in Flakaliden. Both Hyytiälä and Huhus had maximum respiration rates during the summer, typically in the order of $0.25\ mg\ CO_2\ m^{-2}\ s^{-1}$; that is similar to those at Knottåsen but higher than Asa and Flakaliden. Both Hyytiälä and Huhus are thin forests of about the same LAI as those studied here. When comparing the half-hourly rates with a Siberian pine forest as well (Lloyd et al. 2002) and with a Black spruce and Jack pine forest in Canada (Griffis et al. 2003), seasonal pattern and magnitude of maximum net uptake and respiration rates are quite similar.

Fig. 4 Daily component fluxes for 2001 and 2002 in Flakaliden (top) and Knottåsen (middle) and for 2002 in Asa (bottom), respectively



The seemingly small differences between the sites when comparing short time scales becomes, however, of critical importance when considering longer periods such as months and years. The respiration during the winter is of particular importance for the annual budget since the period is quite long. The difference between the sites is most clearly seen in the monthly values (Fig. 7) where Asa and Knottåsen show similar magnitude during the winter, which is much higher as compared to Flakaliden. In 2001 the monthly respi-

ration was higher in Knottåsen throughout the year while in 2002; Flakaliden showed the highest respiration during the summer and Asa had the lowest. The year 2001 was extremely wet in Flakaliden and therefore 2002 is probably more typical when comparing the sites. The differences between the sites in respiration rates cannot be explained by the amount of carbon in the soil or by temperature. Asa has an order of magnitude more carbon in the organic layer than the two other sites while Knottåsen has ca 40%

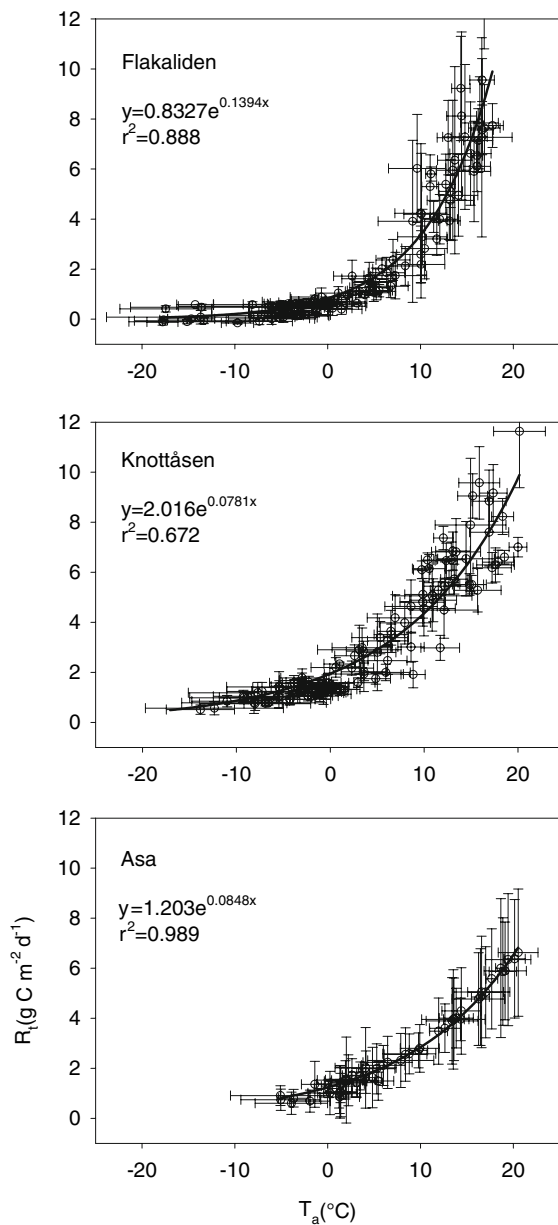


Fig. 5 Mean weekly R_g plotted against the mean weekly air temperature at the three sites. The error bars represent ± 1 standard deviation of the respective values

higher organic layer carbon content than Flakaliden (Table 1). The summer temperature in 2002 was highest in Asa followed by Knottåsen and then Flakaliden. This is opposite to the summer respiration rates but can be understood when considering the differences in temperature sensitivity and base respiration rates (Fig. 5). The high temperature sensitivity

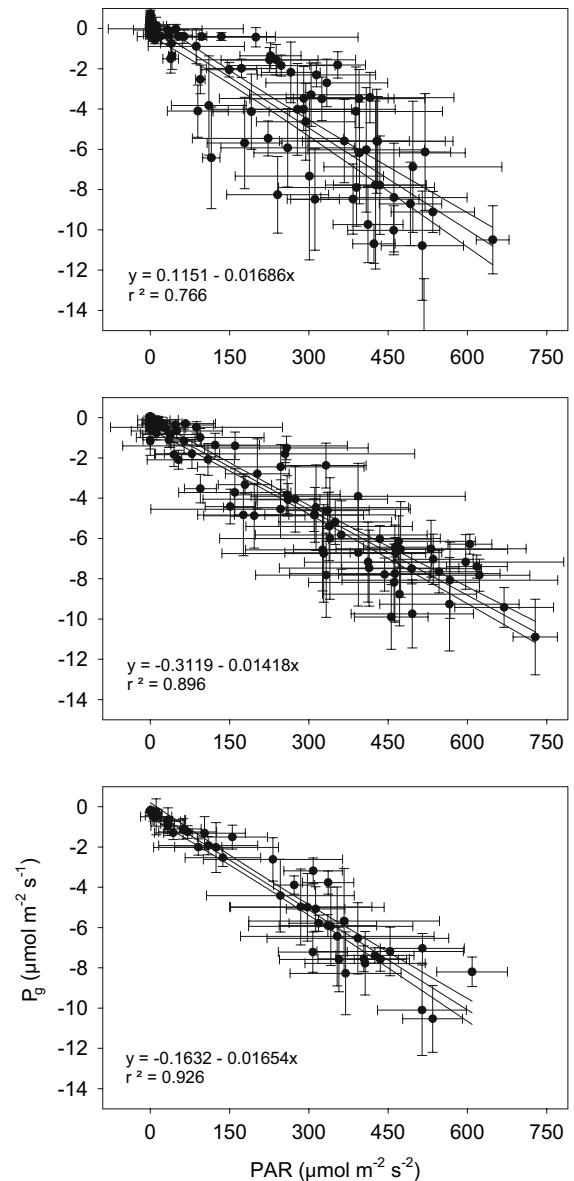
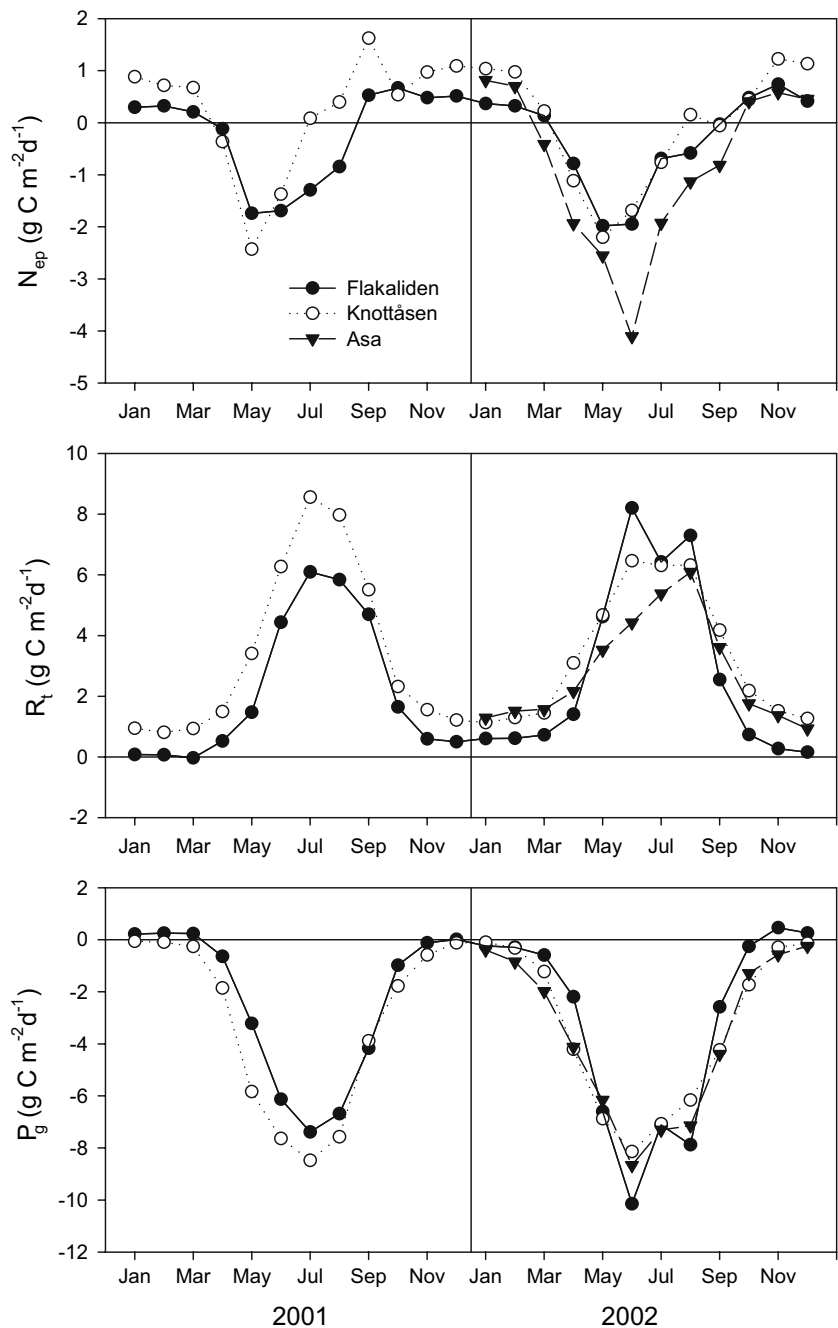


Fig. 6 Mean weekly gross primary productivity plotted against mean weekly PAR at the different sites. The error bars represent ± 1 standard deviation of the respective values

at Flakaliden can explain why this site showed the highest respiration rate during summer and the higher base respiration rate at Knottåsen explains why this site showed higher respiration rate as compared to Asa in spite of similar temperature sensitivities. The behaviour is, thus, logical from the point of view of their respective response functions but it does not explain why the site with the highest carbon content

Fig. 7 Mean monthly N_{ep} for all sites (top), R_t (middle) and P_g (bottom)



showed the lowest respiration rate. All soils are well drained, even the organically rich soil in Asa where a system of ditches gives effective drainage. The results are contradictory in the sense that the organically rich well-drained soil in Asa was expected to have the highest decomposition rates since good aeration of a soil with high organic content provides

the energy needed for the decomposers. Data on ground water level in Asa (data not shown) confirmed that the soil was well drained. One possible explanation for the low respiration rates in Asa could be that the peaty topsoil actually exhibited drying since the capillary rise is much poorer in such a soil as compared to the other mineral soils and with a low

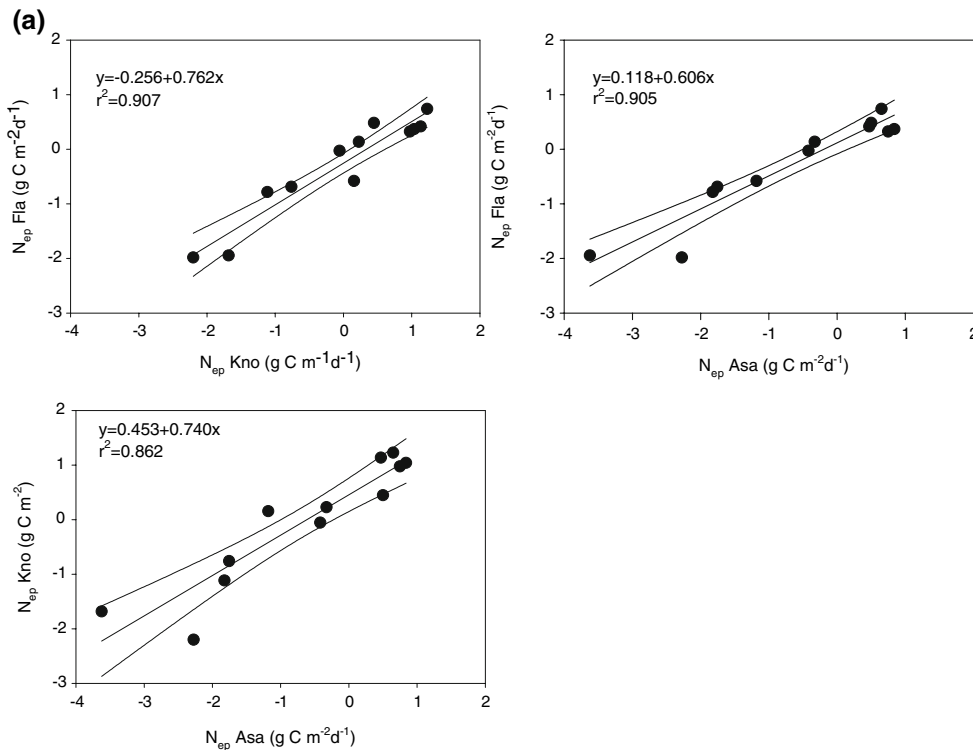


Fig. 8 (a) Relationship between mean monthly N_{ep} for all sites in 2002. Top left: Flakaliden vs. Knottåsen; Top right: Flakaliden vs. Asa and bottom left: Knottåsen vs. Asa, (b) Same as in a) but for R_t and (c) Same as in a) but for P_g

ground water level, the water supply to the soil layer containing most of the roots might become limited. Indications of such drying, with associated lowering of the respiration rates, was observed in a chamber experiment performed in 2005 (L. Klemetsson, unpublished data).

There is surprisingly strong connectivity between the sites concerning monthly mean values. The net ecosystem exchange at one site explains 86% to 91% of variation at other sites (Fig. 8a). The relationship seems to be most linear for N_{ep} than for R_t (Fig. 8b) and for P_g (Fig. 8c). Granier et al. (2002) found, similar, very high correlation between N_{ep} for one beech site in Denmark (Sorø) and the other one in France (Hesse, also beech) when the average time was increased to 10 days. The two curves of 10-day moving average of N_{ep} for 3.5 years were almost indistinguishable. This is probably an effect of a combination of the synoptic weather scale and the relatively long temporal scale resulting in, on average, similar local weather conditions at all sites, which in turn affect respiration (temperature, humidity) and uptake (radiation) similarly.

The sites showed a large difference in annual net ecosystem productivity ranging between a large source for Knottåsen in 2001 with 75–88 g C m⁻² year⁻¹ emitted to the atmosphere and a large sink for Asa in 2002 with –287 to –315 g C m⁻² year⁻¹ in uptake. We can compare this with Hyytiälä which ranged in uptake between –171 and –239 g C m⁻² year⁻¹ during the period 1997 and 2001 (u* method, Suni et al. 2003) and Huhus which had annual uptake rates between –101 to –205 g C m⁻² year⁻¹ during 1999–2002 (Zha et al. 2004). The Siberian pine stand according Lloyd et al. (2003) showed uptake of ca –150 g C m⁻² year⁻¹ in 1999 and 2000 and the Black spruce and Jack pine according Griffis et al. (2003) showed annual uptake of ca –35 respectively –78 g C m⁻² year⁻¹. In Sweden, the Norunda site which consists of a ca 100-year-old mixed pine and spruce forest, range between balance and a source of ca 160 g C m⁻² year⁻¹ (Valentini et al. 2000 and unpublished data).

There is no simple explanation for the large variation in net ecosystem productivity but most of

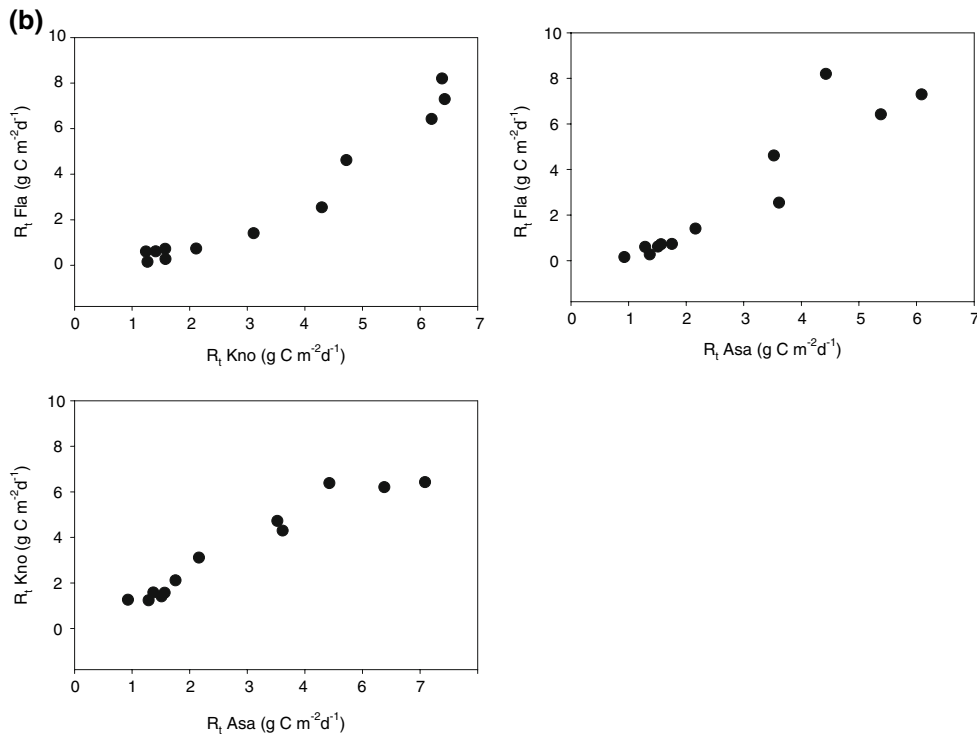


Fig. 8 continued

the explanation can be found in the differences in respiration. The gross primary productivity showed very similar responses to PAR, with only slightly lower light use efficiency for Knottåsen which also had slightly lower canopy mass (Table 1) as compared to Flakaliden and Asa. The differences in gross primary productivity was thus mainly controlled by differences in absorbed PAR and combining this with the differences in the ecosystem respiration, with a high temperature sensitivity for the latter, it is not unexpected that the net ecosystem productivity can vary considerably between years.

The annual gross primary productivity ranged between -875 and $-1317 \text{ g C m}^{-2} \text{ year}^{-1}$ with the lowest for Flakaliden in 2001 and the highest for Asa in 2002. Comparing 2002 only, the difference was smaller with the range being -1136 to $-1317 \text{ g C m}^{-2} \text{ year}^{-1}$. The lower value for Flakaliden in 2001 can be explained by the lower amount of absorbed radiation (Fig. 9) because of the rainy weather that year. The absorbed PAR during the growing season seems to be well related to P_g for all sites. The P_g values found here are slightly higher than those for

the pine forest in Huhus in Finland where the range for the years 1999–2002 was -692 to $-1084 \text{ g C m}^{-2} \text{ year}^{-1}$ and also much higher compared to the Siberian pine forest which had ca $-600 \text{ g C m}^{-2} \text{ year}^{-1}$ (Lloyd et al. 2002). The Siberian forest has a shorter growing season, which probably explains its lower P_g since the daily incoming radiation during the growing season is similar to our sites. Ryan et al. (1997) obtained values of ca $-720 \text{ g C m}^{-2} \text{ year}^{-1}$ for four coniferous forests in Canada as part of the BOREAS study which also are lower than the values found for our sites.

The relationship between P_n and P_g was not very good with only ca 38% of the variation explained (Fig. 9b) and the ratio between P_n and P_g varied between 0.31 and 0.43 (Table 4) with the average being 0.37. Thus, the proportion of P_g lost as autotrophic respiration is on average 63%. This is comparable to other boreal forests in Canada (Ryan et al. 1997) and Siberia (Lloyd et al. 2002). The fraction of P_g going into total biomass varied between 0.12 and 0.25 (Table 4) with the average being 0.17. The difference between net ecosystem production and

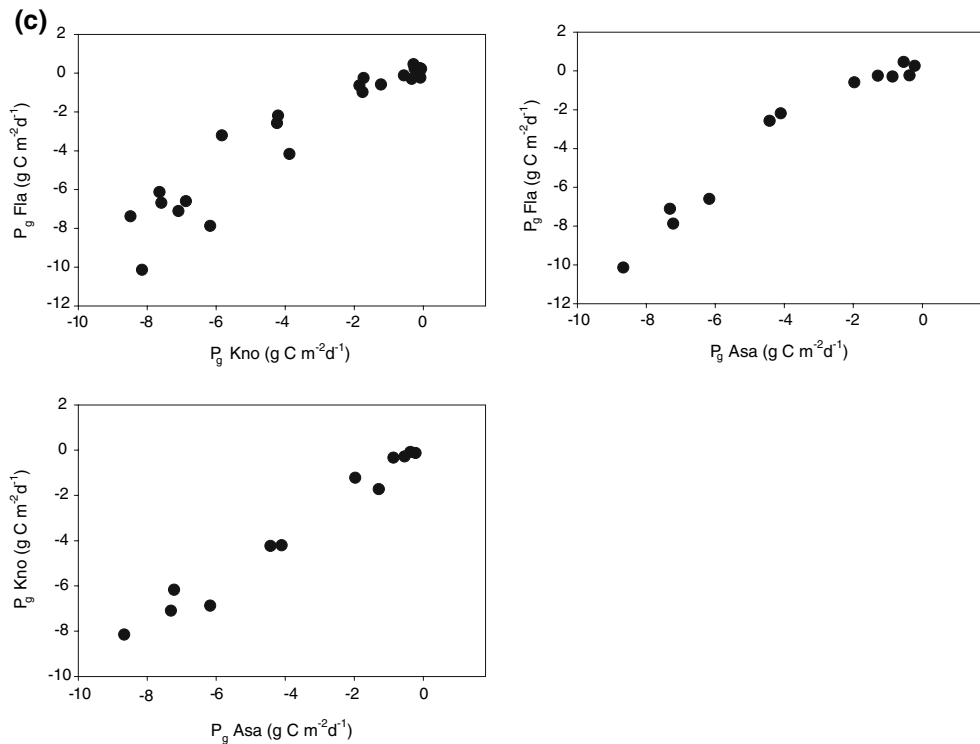


Fig. 8 continued

the biomass production corresponds to the amount of carbon going into soil storage. Surprisingly, all sites lost significant amounts of carbon every year (Table 4) with a mean annual loss of $118 \text{ g C m}^{-2} \text{ year}^{-1}$. These results are not consistent with other estimates based on inventory or modelling results which generally show that the carbon content in organic layers are increasing in southern Sweden and being more or less in balance in northern Sweden (Svensson et al., [this volume](#)).

Akselsson et al. (2005) reported an increase in soil carbon ranging between $4 \text{ g C m}^{-2} \text{ year}^{-1}$ and $41 \text{ g C m}^{-2} \text{ year}^{-1}$ in a gradient from north to south. Their results were based on needle litterfall data and on the concept of the limited value, which gives an estimate of recalcitrant litter, remains. One factor that is often omitted in inventory (or modelling) methods is the changes in carbon content in coarse debris and stumps. It has been estimated that the decomposition of stumps

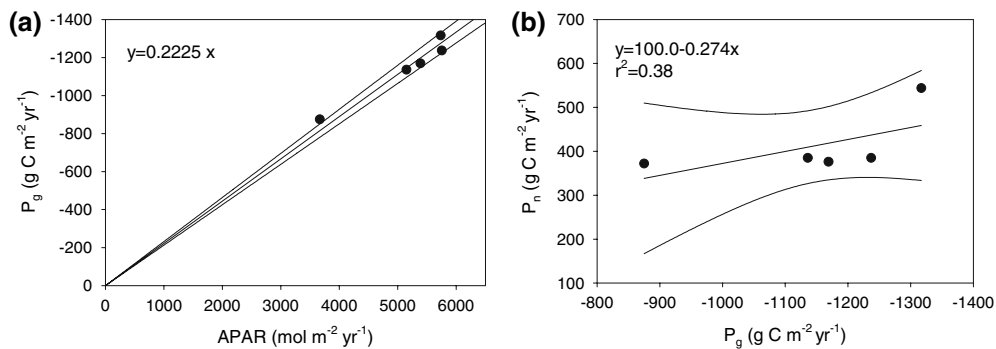
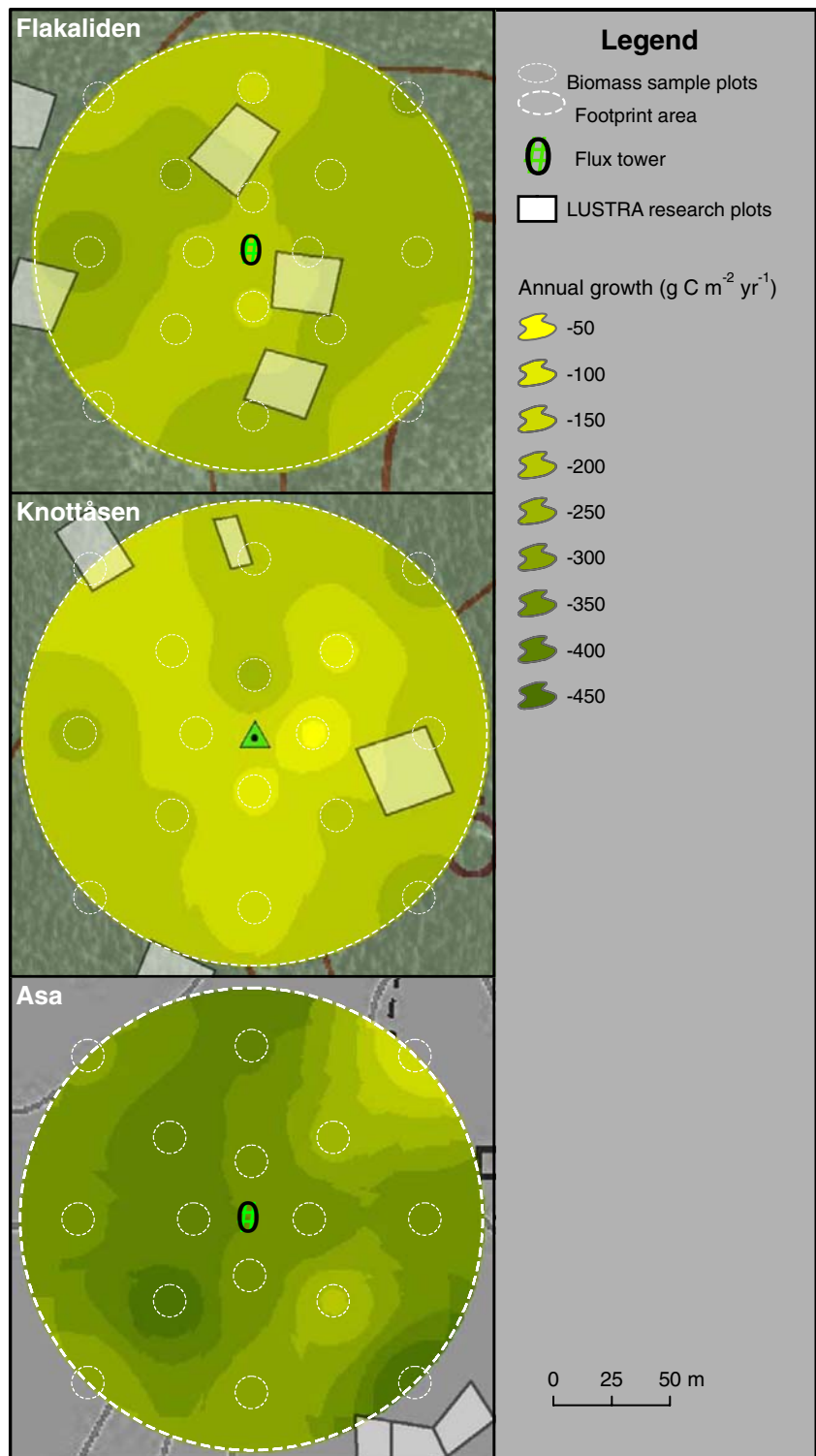


Fig. 9 (a) Relationship between P_g and accumulated absorbed photosynthetic active radiation (APAR) during growing season ($T > 5^\circ\text{C}$) and (b) between P_n and P_g

Fig. 10 Mean annual biomass increment distribution within the 100 m radius areas of the flux towers in Flakaliden (top), Knottåsen (middle) and Asa (bottom)



might account for $20 \text{ g C m}^{-2} \text{ yr}^{-1}$ (Ågren et al. 2007). This does not explain the whole difference between estimates of soil carbon changes based on eddy covariance and biomass increment methods but it is important to understand the difference between methods. Flux measurement does take into account all sources and sinks in the ecosystem, which are very hard to measure by inventory methods. The results cannot be explained by measurement errors since our total errors, which are the sum of the errors in the flux measurements and in the biomass measurements, are much smaller than the difference between annual N_{ep} and P_B .

The most likely explanation for the large loss of soil carbon which we observe is probably because of the years studied being considerably warmer than normal causing a higher than normal total ecosystem respiration. Unfortunately we cannot say whether the absorbed radiation was also higher during these years since we do not have a long time series of this variable to compare with. The other studies referred to above (Svensson et al., [this volume](#); Akselsson 2005), which contradict our results, do not consider the climate for the specific years studied here and considering the large climatic sensitivity that we have shown, it is likely that our results are the results of the specific climatic conditions that occurred during these years. A recent report by the Swedish Meteorological and Hydrological Institute (SMHI 2006) shows that the climate has indeed become ca 1°C warmer during the last 15 years (1991–2005) compared to the long term average (1961–1990), with most of the warming occurring in the winter. It also shows that precipitation has increased, more in the north than in the south. Thus, our results might be an effect of the ongoing warming and if they are generally applicable, they indicate a weakening of the carbon sink in the soil, which might lead to positive feedback to the climate system.

Conclusions

The main conclusions of our comparison of net ecosystem exchange in three forests of the same age and species in Sweden are:

- net ecosystem productivity can differ a lot between sites and between years; from a sink of

about $-300 \text{ g C m}^{-2} \text{ year}^{-1}$ to a source of about $80 \text{ g C m}^{-2} \text{ year}^{-1}$.

- the combination of high soil carbon content, warm climate and drained soils does not necessarily result in higher respiration as compared to the other forests.
- all soils are losing carbon, some at very high rates. The most likely reasons for this is the higher than normal temperature and increased respiration.
- the mean quotient between net primary and gross productivity gives an autotrophic respiration fraction of 63% which is consistent with other boreal forests

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