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Forest floor versus ecosystem CO_2 exchange along boreal ecotone between upland forest and lowland mire

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ABSTRACT

We determined the landscape variation of forest floor (FF) CO_2 uptake (photosynthesis, P), FF CO_2 emission (respiration, R) in relation to net ecosystem CO_2 exchange (NEE) and environmental factors along a forest-mire ecotone in Finland. The 450 m long ecotone extended from xeric, upland pine dominated habitats, through spruce and transitional spruce-pine-birch forest, to sedge peatlands downslope. The CO_2 fluxes were measured at nine stations during 2005 using chamber and IR techniques. Instantaneous P and R measurements for each station were interpolated by fitting their response to continuous records of light (mean $R^2 = 0.66$) and temperature (mean $R^2 = 0.77$) recorded nearby to give annual estimates. Stand biomass increment was used to estimate the annual CO_2 exchange contribution of the trees. Annual *P* values from -307 to -1632 $gCO_2m^{-2}yr^{-1}$ were inversely correlated with FF light ($r = -0.96$), FF above-ground biomass ($r = -0.92$) and canopy openness ($r = -0.95$). Annual R values from 1263 to 2813 gCO_2 m^{-2} yr^{-1} were correlated with tree stand foliar biomass ($r = 0.77$). Estimated NEE values varied from 546 to -1679 gCO_2m^{-2}/yr^{-1}, with *P* contributing from -307 to -1632 $gCO_2m^{-2}yr^{-1}$ (4–90%) to gross ecosystem photosynthetic production, and R from 1263 to 2813 $gCO_2m^{-2}yr^{-1}$ (70–98%) to gross ecosystem respiration (GR).

1. Introduction

The boreal landscape has been highly eroded by glaciations and typically has low relative relief, shallow upland mineral soils and peatlands in lower depressions (Granö et al., 1952). Soil development is related to relief and a sequence of soil types (catena) are shown along slopes. Similarly, the forest and ground vegetation shows a transition downslope. Upslope, xeric pine dominated forests on iron podsols give way to wetter spruce habitats with gleyic soils, then to mixed pine–spruce–birch forest with peaty (histic) soils, and eventually to water saturated peat (histosols) with sparse tree cover. The estimated area of forested mire margins (area >20 ha, peat thickness <30 cm) in Finland is 3.1Mill.ha, and there are 5.1Mill.ha of forested peatlands (area > 20 ha and peat thickness >30 cm) (Lappalainen and Hänninen, 1993).

The transition zone between upland and peatland may be very dynamic in terms of fluctuating environmental conditions and to show high species richness. Large differences in greenhouse gas (GHG) fluxes in transition zones may also be expected to occur. Although small in area, it may play an important role in regional GHG dynamics. For example, the lower flooded littoral zone of shore-lake margin has been shown to act as a sink for atmospheric CO_2 while the upper littoral to act as a net source of CO_2 (Larmola et al., 2003). Most GHG studies have ignored transition zones, preferring to concentrate on typical upland (Pumpanen et al., 2003; Kolari et al., 2004) or typical peatland conditions (Alm et al., 1997; Nykänen et al., 2003).

The net ecosystem production (NEP) of upland forests is approximately the difference between the net primary production (NPP) of trees and forest floor (FF) vegetation and heterotrophic respiration (Liski et al., 2006). Kolari et al. (2006) found that CO_2 uptake of the FF vegetation in an upland Scots pine forest contributed 13% to the ecosystem annual gross photosynthetic production (GPP). In peatlands, the growth of trees is limited by water table depth (Pepin et al., 2002), and carbon accumulation is mostly that of ground vegetation (Turunen et al., 2002). The net flux of CO_2 from a particular ecosystem depends on the balance between the uptake of atmospheric CO_2 by vegetation (photosynthesis) on the one hand, and the autotrophic and

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heterotrophic emissions of CO_2 to the atmosphere (respiration) on the other. The carbon balance of forests is mainly controlled by temperature (Valentini et al., 2000), with soil moisture only becoming important under very dry or very moist conditions (Minkkinen and Laine, 1998; Pumpanen et al., 2003; Tuittila et al., 2004; Weimin et al., 2006). Soil respiration is mainly dependent on the recent photosynthesis of living biomass (Högberg et al., 2001; Janssens et al., 2001), and on moisture conditions if they inhibit primary production.

The aim of our study was to determine annual FF and whole ecosystem carbon balance at nine sites along an upland forest–peatland toposequence in the boreal zone. We hypothesized that the annual carbon balance of the FF would vary spatially in relation to a number of environmental factors, nutrient status, and water table depth. The greatest spatial variation was expected to be found in the forest-mire transitional zone.

2. Materials and methods

2.1. Study ecotone

A forest-mire ecotone forming a continuum of plant communities, soil moisture and nutrient conditions was identified near to the Hyytiälä Forestry Station in Central Finland (61°47′, 24°18′). The forest-mire ecotone was 450 m long with a relative relief of 15 m and a slope 3.3% facing North East (Fig. 1). The forest types ranged from Scots pine forest through more fertile pine–spruce forest and spruce dominated type to paludified mixed spruce forest, and finally to a tall-sedge pine fens (Table 1). The ecotone is 6 km apart to the station for continuous measurements of forest-atmosphere relations (SMEAR II) recorded since 1996 (http://www.honeybee.helsinki.fi/smear) (Vesala et al., 1998; Mäkelä et al., 2006). Ecotone and SMEARII data of environmental factors like the light above canopy, soil moisture and temperature are strongly correlated.

2.2. Field measurements and sampling

Nine stations were established, four situated in upland forest, two in forest-mire transition and mire margin and three in forested peatlands (Fig. 1, Table 1). At each sampling stations three steel collars (31.5 cm in diameter, 5 cm deep) were installed 1–3 m apart, and into the moss layer, just above the roots of ground vegetation (Fig. 2).

A closed flow-trough chamber was fitted to the collar to measure CO_2 efflux repeatedly. The measurements were taken once a week during the growing season 2005 (May–November), and once in a month in winter. On each occasion the measurements were made between 8 am and 5 pm and the order in which each station was measured was random. Measurements were made with a portable infrared CO_2 analyser (EGM4, SRC-1 PP systems Inc.) fitted to modified closed soil respiration chambers (transparent and non-transparent, volume 21.2 L) (Fig. 3). The CO_2 flux was calculated automatically as the slope of a linear fit to 25 concentration readings at 4.8 second intervals within a 120 second measuring period. Twenty-five CO_2 concentrations were recorded for each gas exchange measurement and subsequently used for evaluation of linearity and data quality. We first measured the net forest floor exchange CO_2 flux (NFFE) with the transparent chamber, and total FF respiration (R) immediately after with the non-transparent chamber. Photosynthesis (P, negative sign), carbon fixation of the ground vegetation was subsequently calculated as the difference between NFFE and R.

Simultaneously with the CO_2 flux measurements, soil temperatures at 5, 15 and 30 cm depth were also measured using permanently installed thermocouples. Soil temperature at 5 cm

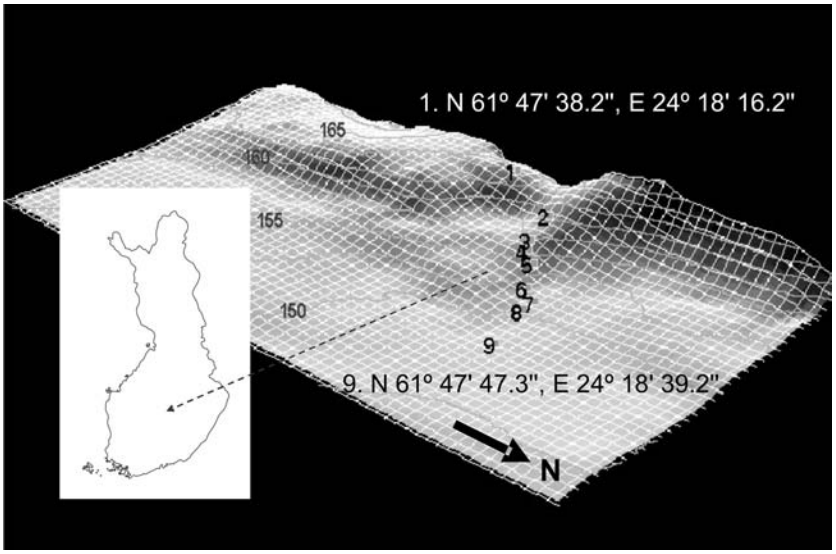

Fig. 1. Spatial distribution of nine studied forest types on Northern slope of glacial esker 'Vatiharju' in central Finland. The map of Finland and digital elevation model with contour lines and site numbers; (Upland forest types: 1 CT – *Calluna,* 2 VT – *Vitis Idea,* 3 MT – *Myrtilus,* 4 OMT – *Oxalis-Myrtillus;* Forest – mire transition and mire margin types: 5 OMT+ – *Oxalis-Myrtillus Paludified, 6* KgK – *Myrtillus Spruce Forest Paludified*; Open mire types: 7 KR – *Spruce Pine Swamp, 8 and 9* VSR – *Tall Sedge Pine Fen*); coordinates in Finnish Geographical Coordinate System. The catena of 450 meters represents moisture and fertility gradient based on classification, English names and acronyms of Cajander (1949), and Laine et al. (2004).

Table 1. Study site characterisctics

Characteristic	Station								
	1	2	3	4	5	6	7	8	9
Site type[a]	CT	VT	MT	OMT	OMT+	KgK	KR	VSR1	VSR2
Elevation, m a.s.l.	164	160	157	156	154	152	151	150	149
Slope position	Crest	Upper Slope	Middle Slope	Middle Slope	Lower Slope	Lower Slope	Toe	Toe	Level
Slope, °	2.3	3	3.5	4	3.5	2.9	1	1	0.3
Aspect, °	27	103	70	50	30	18	70	85	62
Soil type[b]	Haplic podzol	Haplic podzol	Haplic podzol	Haplic podzol	Histic podzol	Gleyic histic podzol	Hemic histosol	Hemic histosol	Hemic histosol
Humus layer or peat thickness, m	0.07	0.08	0.07	0.12	0.15	0.32	0.78	1	1.2
Stocking density, stems ha^{-1}	600	2050	925	650	400*	1825	1300	900	275
Basal area, m^{-2} ha^{-1}	33.6	38.9	41.6	51.0	14.4	41.2	15.4	8.4	1.7
Canopy openness,%	37	26	18	20	21	22	24	50	80
Stand biomass[c], kg m^{-2}	20.7	23.6	32.5	46.0	11.2	26.8	7.5	3.1	0.5
Pine,% (age, yr)	96 (100)	75 (100)	0	0	0	32 (130)	75 (130)	95 (110)	100 (100)
Spruce,% (age, yr)	4 (30)	25 (30)	95 (90)	99 (80)	68 (70)	41 (120)	14 (60)	1	0
Birch,% (age, yr)	0	0	5 (95)	1	32 (85)	27 (120)	11 (100)	4 (60)	0
Ground vegetation biomass[d], g m^{-2}	181	130	165	52	135	190	162	360	550
Soil temperature at 5 cm [°C]	5.7	5.2	5.3	4.9	5.2	5.6	5.1	5.7	5.1
Water table depth [cm]	881	217	69	65	33	19	19	7	8

[a]CT: Calluna vulgaris type; VT: Vaccinium vitis-idaea type; MT: Vaccinium myrtillus type; OMT: Oxalis acetosella-Vaccinium myrtillus type; OMT+ : Oxalis acetosella-Vaccinium myrtillus, paludified type; KgK: Myrtillus Spruce Forest, Paludified; KR: Spruce Pine Swamp; VSR: Tall Sedge Pine Fen (Cajander 1949; Laine et al., 2004).
[b]IUSS Working Group WRB (2006), [c]above- and below-ground biomass, *exceptionally low because of windblown trees, [d]above-ground biomass only.

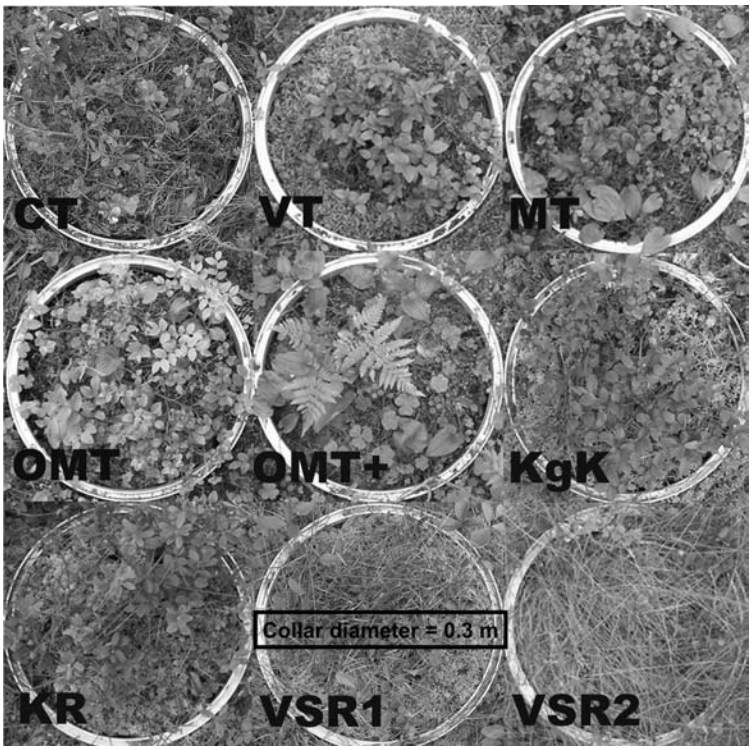

Fig. 2. Forest floor species comparison along the catena (one study plot per site) of nine studied forest types. For forest type acronyms, see Table 1.

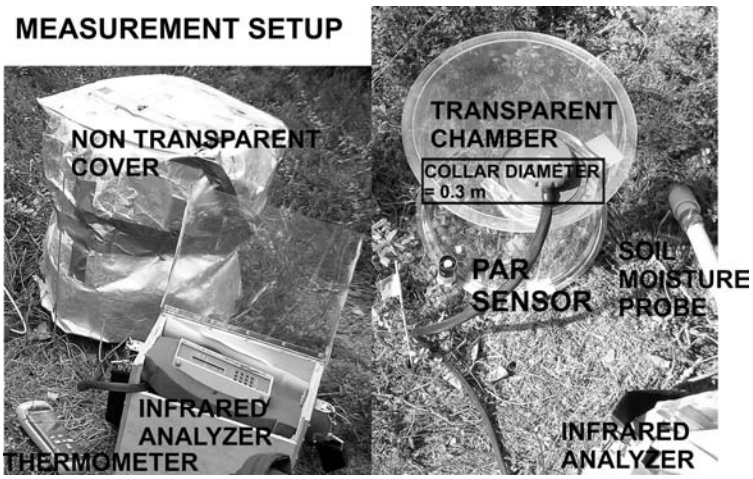

Fig. 3. Closed chamber setup to measure total respiration (R) (left), and net CO_2 exchange of forest floor (NFFE) [g m^{-2} h^{-1}] (right). Fluxes were obtained directly during the measurement intervals, and at the end from IR analyser. Location of sensors is demonstrated by annotations.

depth (T_5) was also recorded continuously at 3 hours intervals during the period from 1 January to 31 May, and at 1 hour intervals during 1 June to 12 October with permanently installed sensors (DS1920 Temperature iButton® – Maxim/Dallas Semiconductor). Missing soil temperature data at the end of season (13 October to 31 December) for all stations were filled with soil temperature records from nearby micro-meteorological stations (upland forest SMEARII and lowland mire Lakkasuo).

Photosynthetically active radiation (PAR) reaching the FF was recorded with portable Delta-T PAR sensor and delta data logger. We placed the PAR sensor in a spot considered the most representative of light conditions nearby the chamber. Volumetric soil moisture at 10 cm depth (SM10) was measured with portable Delta-T ThetaProbe (calibrated for each soil type) inserted into diagonally installed polyvinylchloride perforated tubes. To make annual estimates, SM10 measurements at the study stations were calibrated with continuous hourly records of soil moisture recorded at the SMEARII station. Water table depth (WT) was measured weekly during the vegetative period from vertically installed perforated plastic tubes. To give the annual estimates, the WT measurements at the study sites were calibrated with continuous hourly seasonal records of WT recorded at a ground water well located 100 m away in the open peatland Lakkasuo.

The ground vegetation at each collar was photographed with digital camera nine times during growing season 2005. The images were analysed for proportional development of leaf (photosynthesizing) area and non-leaf (not photosynthesizing) area using geographic information software (ArcInfo9). The tree stand canopy for each station was photographed once using a 'fish eye' lens, and canopy openness estimated using Gap Light Analyser (GLA) software (Frazer et al., 1999). Above-ground FF biomass was determined in July 2004 for each station by harvesting three 0.07 m^2 sample plots located near to the measuring collars, oven drying and weighing. Total above- and below-ground biomasses of trees were estimated from June 2005 measurements of breast height diameter (dbh), height, and canopy lengths and applying Marklund's allometric biomass functions (Marklund, 1988). The mean age of the trees was estimated by counting the annual internodes from photographs of tree stands.

A digital elevation model (Fig. 1) was reconstructed with map elevation points in ArcInfo9. The study stations were positioned with global positioning system to determine the position, elevation, slope and aspect of each station.

3. Integration of CO_2 exchange measurements

FF CO_2 uptake (P, ground vegetation photosynthesis, a negative sign) was calculated as a difference between net forest floor CO_2 exchange (NFFE) and FF CO_2 emission (R, autotrophic and heterotrophic respiration, a positive sign) (eq. 1). Positive values of NFFE indicate a net CO_2 emission to the atmosphere (i.e. FF is a source) and negative values of NFFE indicate a net uptake of CO_2 (i.e. FF is a sink).

$$\mathrm{P} = \mathrm{NFFE} - \mathrm{R} \tag{1}$$

The half an hour values of P and R derived from measurements for each collar were subsequently used for non-linear regressions to interpolate P, R and NFFE values during whole year. The simulated values were then summed to give the annual value for each collar.

3.1. Photosynthesis model

For each of 27 sample plots, the measurements of P were fitted to those of *PAR* using Michaelis–Menten function and proportional leaf area development *LA* (eq. 2).

$$\mathrm{P} = \left(\frac{P_{\max} PAR}{PAR + b}\right) LA, \tag{2}$$

where *PAR* is the mean photosynthetically active radiation [μmol $m^{-2}s^{-1}$] reaching the FF; $P_{\max}$ is maximum potential photosynthesis [g CO_2 $m^{-2}h^{-1}$] limited by light saturation; b is the PAR level, when photosynthesis is half the maximum value. Equation was fitted for each sample plot in each station (20 measuring occasions, 27 collars in nine stations). Parameters $P_{\max}$ and b for each studied sample plot are in Table 2. Each forest floor P being 30 min (half an hour) averages. Tree stand average PAR levels were estimated using a stand photosynthesis model (Mäkelä et al., 2006) the stand characteristics (Mäkelä et al., 2006; Mäkelä, 1997), and continuous above-canopy PAR measurements recorded 6km distant at the SMEARII environmental monitoring station.

We modelled LA [%] during growing season 18 April to 21 November 2005 by fitting ArcInfo9 measurements to lognormal function, with faster increase in early summer and gradual decline in autumn (Wilson et al., 2006) (eq. 3).

$$LAi = LA_{\max} \exp\left(-0.5\left(\frac{\ln\left(\frac{day}{x_{\max}}\right)}{b}\right)^2\right) \tag{3}$$

Where, LA_i is leaf area projection for i^{th} sample plot, $LA_{\max}$ is maximal leaf area projection and $x_{\max}$ is the day of year when it occurs, *day* is Day of year, and b is the parameter. Length of growing season starts 18 April and ends 21 November 2005. It is determined by snowmelt in spring and permanent snow cover in winter measured at SMEARII located 6 km NW. The start of the growing season was taken to be the moment when the daily average temperature of the soil humus layer was permanently above 0 °C.

3.2. Respiration model

Total respiration [g CO_2 $m^{-2}h^{-1}$] was modelled for each collar by fitting measurements of respiration fluxes to soil temperatures at 5 cm depth using the exponential function reported by Lloyd and Taylor (1994) (eq. 4).

$$R = R_T \exp\left(b\left(\frac{1}{56.02} - \frac{1}{T_5 + 46.02}\right)\right) \tag{4}$$

Where T_5 is the soil temperature in 5 cm [°C], and R_T is respiration level at site reference temperature [g CO_2 $m^{-2}h^{-1}$], b[K] activation energy divided by gas constant (parameters for individual sample plots are in Table 2). The reference temperature T_{ref} is 283.15 °K, T_o is 227.13 °K, and the given constants (56.02 and 46.02) are result of using T_5 in °C. Respiration over the year was calculated by continuously integrating measured temperatures at 5 cm at the stations.

3.3. Calculation of Net ecosystem CO_2 exchange

Annual Net ecosystem CO_2 exchange (NEE) [g CO_2 m^{-2} yr^{-1}] was calculated by summing simulated values of R and P(P, negative values for CO_2 uptake), gross increment of tree stand biomass converted to stand net photosynthetic production (NPPt, negative values for CO_2 uptake) and estimated respiration of tree roots (Rtr) (eq. 5).

$$\mathrm{NEE} = \mathrm{NPPt} - \mathrm{Rtr} + \mathrm{R} + \mathrm{P} \tag{5}$$

Table 2. Forest floor photosynthesis and respiration (eq. 2 and 4), non-linear regression model R^2, parameters and their estimation errors (± standard deviation SD, and standard error SE) for each of the nine study stations (CT, VT, MT, OMT, OMT+, KgK, KR, VSR1, VSR2, see Table 1 for forest-type acronyms)

CO_2 exchange component and model parameter	Statistic	Station (and site type)								
		1(CT)	2(VT)	3(MT)	4(OMT)	5(OMT+)	6(KgK)	7(KR)	8(VSR1)	9(VSR2)
Photosynthesis, obs/pred	R^2	0.603	0.646	0.629	0.608	0.586	0.474	0.726	0.855	0.85
P_{max}, g CO_2 m^{-2} h^{-1}	Mean	−0.012	−0.015	−0.009	−0.007	−0.007	−0.005	−0.011	−0.027	−0.043
	SD	±0.002	±0.008	±0.004	±0.006	±0.002	±0.002	±0.001	±0.004	±0.010
	SE	0.003	0.008	0.003	0.002	0.003	0.003	0.003	0.004	0.009
b, mmol m^{-2} s^{-1}	Mean	0.076	0.157	0.080	0.049	0.084	0.042	0.105	0.290	0.487
	SD	±0.006	±0.118	±0.047	±0.083	±0.007	±0.034	±0.020	±0.084	±0.205
	SE	0.049	0.131	0.05	0.033	0.068	0.048	0.058	0.091	0.195
Respiration, obs/pred	R^2	0.743	0.883	0.821	0.804	0.768	0.803	0.717	0.742	0.719
R_T, g CO_2 m^{-2} h^{-1}	Mean	0.380	0.269	0.299	0.498	0.339	0.334	0.391	0.205	0.259
	SD	±0.068	±0.024	±0.016	±0.069	±0.036	±0.069	±0.083	±0.041	±0.053
	SE	0.028	0.012	0.014	0.025	0.017	0.022	0.028	0.02	0.034
b, K	Mean	349.6	411.6	401.2	344.4	378.6	393.6	506.7	525.1	517.6
	SD	±58.0	±54.1	±30.1	±12.3	±36.7	±36.4	±67.0	±62.7	±106.6
	SE	51.4	41.6	49	47.6	56.9	55.4	86.9	89.6	87.4

Positive values of NEE indicate a net CO_2 emission to the atmosphere (i.e. ecosystem is a source) and negative values of NEE indicate a net uptake of CO_2 (i.e. ecosystem is a sink).

Gross biomass increment of stand [g m^{-2} yr^{-1}] was calculated with measurements of tree dbh, height, mean estimated age of each species and site type using the SIMO simulator (Tokola et al., 2006). Dry biomass was converted to carbon (factor 0.519 for spruce and pine and 0.505 for birch; Karjalainen and Kellomäki, 1996) and to CO_2 mass equivalents NPPt [g CO_2 m^{-2} yr^{-1}]. For the respiration of tree roots we used the ratio of Rtr to autotrophic respiration (Ra) according to Ryan et al., (1997). Ra values were calculated from previously estimated NPPt and from carbon use efficiency (CUE) for spruce, pine and birch corresponding to NSA-OBS, NSA-OJP, and NSA-OA stands found for boreal forests by Ryan et al. (1997).

4. Results

4.1. Variation among forest type environmental conditions

The annual PAR level reaching the FF ranged between 9 and 143 umol$m^{-2}s^{-1}$ and were correlated with the biomass characteristics (e.g. Pearson correlation with canopy openness r = 0.92 and forest stand biomass r = −0.84) (Table 3). Annual PAR under four forest canopies is less than 20% (densest, spruce dominated forest type, OMT just 6%) of maximum incoming light in open mire VSR2 (Fig. 4). Gradient of incoming light on the FF has declining tendency from both ends of the catena towards OMT, towards the more fertile mineral soils and highest amount of tree biomass. Transitional forest OMT+, situated close to upland site OMT, has exceptionally high-annual light level (45% of maximum VSR2), because nearly half of trees were windblown.

The annual average of soil temperature at 5 cm ranged between 4.94 and 5.72 °C. Weekly trends of soil temperatures for all sites are in Fig. 4. Wet peatland sites tend to show a delay in warmed up and cooling in early autumn compared to upland forest sites. Maximum difference in soil temperature among study sites was 2.2 °C during the snow and soil melting period in April. The differences in June, July T5 were rather stable around 1 °C, until beginning of August when the soil temperature difference was declined and stabilized at 0.5 °C in the middle of October until December.

The annual average soil moisture content at 10 cm depth was similar (around 15%) just for the upland mineral soil stations (CT, VT, MT, OMT), but increased considerably further downslope for forest-mire transition types (OMT+ 42%, KgK 69%) Drier forest-mire margin (OMT+) fluctuates between field capacity (surface layer 65%) in wet early and late summer to drier conditions (15%) during summer drought (Fig. 4). Wetter forest-mire margin (KgK) had moisture conditions closer to those of peatlands down the slope (KR, VSR1, VSR2), than to ones of upland minerals soils (CT, VT, MT, OMT). The annual soil moisture contents were negatively correlated with elevation of forest types (r = −0.86) (Table 3). Increasing wetness of soils have shown also good correlation with increasing depth of organic horizons (r = 0.92) (Table 3).

The annual WT depth varied greatly between the stations, ranging from 881 cm (highest upland Scots pine forest on sandy podzol) to 7 cm (lowland tall-sedge pine fen on histosol). Transitional forest-mire sites showed the highest seasonal fluctuation of WT depths, with annual level of 20 cm and a summer minimum as low as 70 cm (Fig. 4).

4.2. Reliability of estimated forest floor CO_2 exchanges

The measurements of FF CO_2 fluxes of forest-mire transition were similar to those of the upland sites, but the CO_2 uptakes of peatlands were generally higher than others (Fig. 5).

The models we used to predict half an hour average FF respiration and photosynthesis values explained around 77% of variance in the corresponding measurements of CO_2 emissions, and around 58% of variance in the CO_2 uptake measurements (Figure 6). The greatest source of error was in modelling the FF light and light response curves. Also difference in time compatibility could be erroneous, when comparing modelled half an hour average to observed data of 120-second interval (especially forest floor PAR). The greatest variation in the annual average net ecosystem CO_2 fluxes was associated with the forest-mire transition stations (Table 4).

4.3. Variation in forest floor CO_2 uptakes (P, negative sign)

There is clear difference in the annual CO_2 uptake between nine stations (Table 4, Figs. 7 and 8). Annual levels of FF CO_2 uptake were strongly correlated to annual levels of PAR reaching the FF (r = −0.96) and FF above-ground biomass (r = −0.92) (Table 3). Higher annual PAR levels reaching the ground vegetation promoted higher CO_2 uptake by FF vegetation. FF above-ground biomass was correlated to intercepted PAR (r = 0.9), and forest floor PAR was correlated to canopy openness (r = 0.92). The *P* values of the nine stations were not significantly correlated to soil temperature at 5 cm depth or to WT depth. The FF photosynthesis contributed from −307 to −1632 g CO_2 m^{-2} yr^{-1} (4–90%) to total forest photosynthetic production (Table 4, Fig. 8).

4.4. Variation in forest floor CO_2 emissions (R)

The annual FF CO_2 emissions showed higher values of the upland forest and forest-mire transitions, and lower values of peatlands (Table 4, Figs. 7 and 8). FF respiration rates were not significantly correlated to soil temperature, soil moisture content or WT depth, but only to the tree stand leaf mass (r = 0.77). Despite the dryness of the pine dominated CT site (deepest WT) with relatively open canopy (forest floor PAR 45% of

Table 3. Pearson Correlations Sig. 2-tailed between annual forest floor CO_2 fluxes, and environmental factors along the forest-mire ecotone for nine forest types

	NFFE	R	P	STANDM	CANOP	LEAFM	GVAM	OH	SM	PAR	ELEV	SLOPE
NFFE	1.000											
R	0.825(**)	1.000										
	0.006											
P	0.856(**)	0.419	1.000									
	0.003	0.262										
STANDM	0.860(**)	0.654	0.811(**)	1.000								
	0.003	0.056	0.008									
CANOP	−0.815(**)	−0.379	−0.951(**)	−0.658	1.000							
	0.007	0.315	0.000	0.054								
LEAFM	0.904(**)	0.766(*)	0.768(*)	0.831(**)	−0.669(*)	1.000						
	0.001	0.016	0.016	0.006	0.049							
GVAM	−0.902(**)	−0.559	−0.925(**)	−0.724(*)	0.952(**)	−0.710(*)	1.000					
	0.001	0.118	0.000	0.027	0.000	0.032						
OH	−0.809(**)	−0.486	−0.862(**)	−0.774(*)	0.794(*)	−0.759(*)	0.850(**)	1.000				
	0.008	0.184	0.003	0.014	0.011	0.018	0.004					
SM	−0.742(*)	−0.526	−0.724(*)	−0.765(*)	0.660	−0.599	0.779(*)	0.922(**)	1.000			
	0.022	0.146	0.027	0.016	0.053	0.088	0.013	0.000				
PAR	−0.865(**)	−0.484	−0.956(**)	−0.838(**)	0.920(**)	−0.708(*)	0.904(**)	0.792(*)	0.726(*)	1.000		
	0.003	0.186	0.000	0.005	0.000	0.033	0.001	0.011	0.027			
ELEV	0.498	0.372	0.447	0.503	−0.406	0.378	−0.553	−0.794(*)	−0.864(**)	−0.444	1.000	
	0.172	0.324	0.228	0.168	0.279	0.316	0.122	0.011	0.003	0.231		
SLOPE	0.820(**)	0.476	0.903(**)	0.845(**)	−0.792(*)	0.842(**)	−.818(**)	−0.916(**)	−0.800(**)	−0.791(*)	0.532	1.000
	0.007	0.195	0.001	0.004	0.011	0.004	0.007	0.001	0.010	0.011	0.141	

**.Correlation is significant at the 0.01 level (2-tailed); *. Correlation is significant at the 0.05 level (2-tailed); NFFE: net forest floor CO2 exchange; R: forest floor respiration; P: forest floor photosynthesis; STANDM: stand biomass; CANOP : canopy openness; LEAFM: stand leaf mass; GVAM: aboveground ground vegetation biomass; OH: depth of organic horizon; SM: soil moisture at 10 cm; PAR: photosynthetically active radiation; ELEV: elevation.

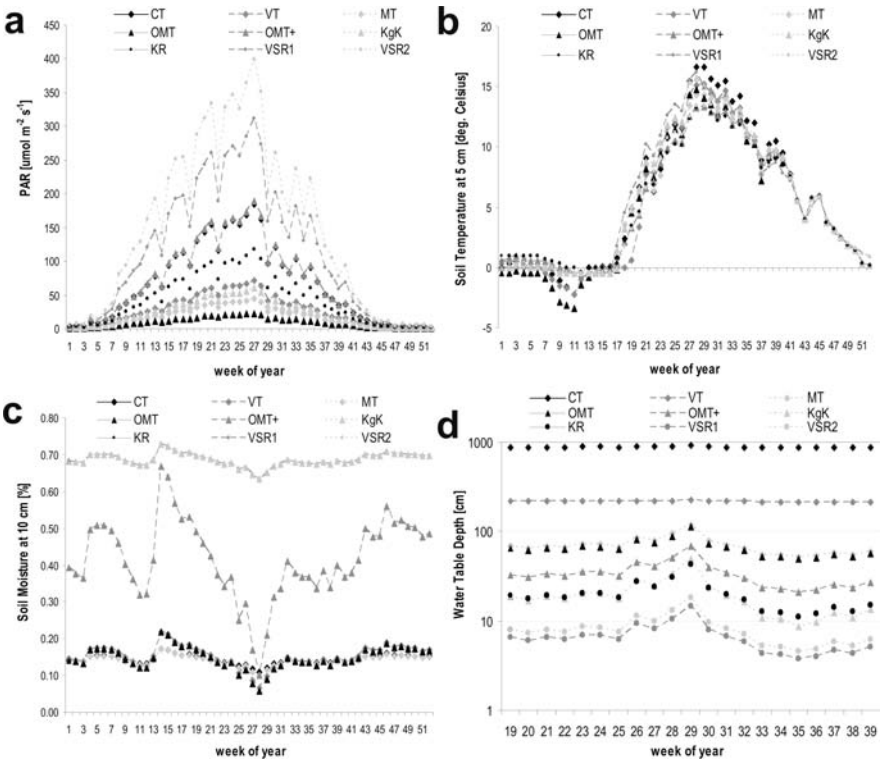

Fig. 4. Time series of weekly environmental characteristics found along the catena during year 2005); (a) integrated forest floor photosynthetically active radiation (PAR) [umol m^{-2} s^{-1}]; (b) measured soil temperature at 5 cm depth [°C]; (c) integrated volumetric soil moisture at 10 cm depth [%] for upland and transitional forest (VSR peatland sites were at 10 cm mostly saturated); (d) integrated water table depth shown in logarithmic scale; For forest type acronyms, see Table 1.

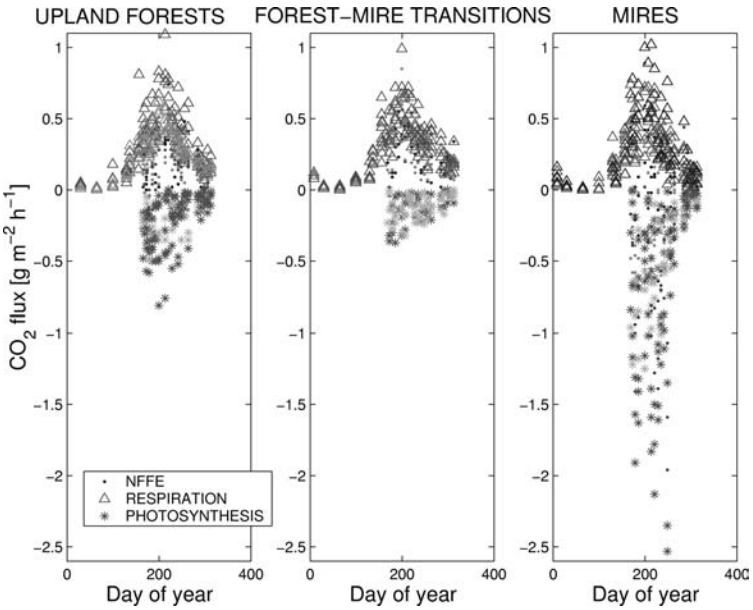

Fig. 5. Forest floor instantaneous (120 seconds) measurements of CO_2 fluxes [g m^{-2} h^{-1}] during year 2005. NFFE and Respiration was measured, Photosynthesis (minus sign for CO_2 uptake) was calculated, as a difference between NFFE and Respiration. Fluxes are grouped to upland forests types (CT, VT, MT, OMT); forest mire transitions (OMT+, KgK); and mire types (KR, two VSR sites). For forest type acronyms, see Table 1.

maximum PAR of VSR2), the annual mean respiration rate of 2401 ± 469 g m^{-2} h^{-1} (Table 4) was 85% of the OMT station, which had the highest emissions. Increasing R/GR ratio from transitions (e.g. OMT+ 78%) towards peatlands (e.g. VSR2 98%) reflects the diminishing role of tree stand and increasing part of the forest soil with ground plants (Table 4, Fig. 8).

4.5. *Variation in net forest floor CO_2 exchanges (NFFE)*

With the exception of the two tall-sedge pine fens, the annual net FF CO_2 exchange was clearly positive (Fig. 8, Table 4). The NFFE of the tall-sedge pine fens were nearly zero (VSR1) or negative (VSR2), indicating the FF was a net sink for CO_2.

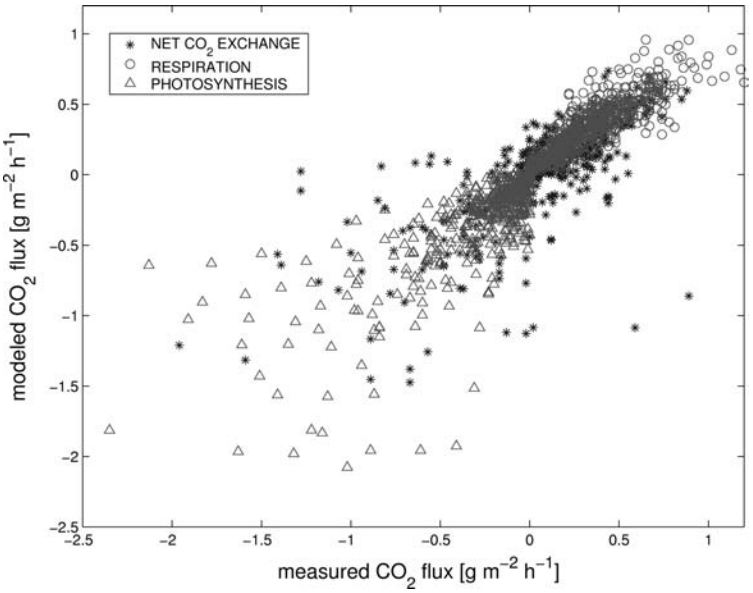

Fig. 6. Evaluation of fit between measured instantaneous CO_2 fluxes [g m^{-2} h^{-1}]; (120 second intervals) and modelled half an hour CO_2 average fluxes [g m^{-2} h^{-1}]; for nine studied forest types. For forest type acronyms, see Table 1, and for regression statistics see Table 2.

However, the balance between CO_2 uptake and efflux varied during the year at all stations. The FF acted as a sink during early spring and late summer at some sites, and in midsummer (with exception of the open mire sites) all the sites acted as net CO_2 sources (Fig. 7). The forest canopy was found to be the main factor controlling FF photosynthesis, respiration and also net forest floor CO_2 exchange (NFFE correlation with canopy openness $r = -0.82$)(Table 3). One of the main features of the ecotone is the marked opening of tree canopy between upper forested-mire margin and lower mire types (Fig. 8, Table 4). The NFFE values are thus seen change from small net emission from FF at the edge of closed forest canopy (KR) to net uptake of CO_2 in open mires with sparse trees (VSR1, VSR2).

4.6. *Variation in net forest ecosystem CO_2 exchanges (NEE)*

After adding the net tree stand exchange to NFFE the resulting NEE values indicated that seven of the stations (VT, MT, OMT, OMT+, KgK, VSR1, VSR2) were behaving overall as CO_2 sinks (-19 ± 732 to -1679 ± 1091 g CO_2 m^{-2} yr^{-1}) and two of the stations (Callunna type Scots pine forest and Spruce pine swamp type forest-mire margin) were sources of CO_2 (respectively, 546 ± 860 and 261 ± 667) (Fig. 8, Table 4). However, there was great within-station variability. Also great estimation errors suggest wide range of NEE values for each ecosystem. Some forest types (VT, MT, OMT, OMT+) were clearly sinks, while CT, KgK, KR and VSR types could be either sinks or sources. Forest floor P fluxes contributed to whole forest GPP from -307 to -1632 g CO_2 m^{-2} yr^{-1} (4–90%) and the R contributed to whole forest gross respiration (GR) from 1263 to 2813 g CO_2 m^{-2} yr^{-1} (70–98%) (Fig. 8, Table 4).The NEE along the forest-mire ecotone was correlated to the amount of spruce ($r = -0.84$) and pine ($r = 0.72$) biomass.

5. Discussion

Net carbon uptake of ecosystems results from large but opposing fluxes of photosynthesis and respiration. In relation to ecosystem carbon uptake and emissions, the net flow may only be a small proportion of them (Lindroth et al., 1998; Markkanen et al., 2001). Studying FF carbon uptake and emissions by indirect chamber measurements helps to understand net ecosystem exchange determined from direct methods (eddy covariance techniques). The annual net FF CO2 exchange values found in our study are in good agreement with the findings reported for similar and nearby ecosystems studied with chamber and eddy covariance measurements. Our NFFE value of -256 ± 208 g CO_2 m^{-2} yr^{-1} for the Tall Sedge Pine Fen, VSR2, with sparse trees compares with the mean value of -430 g CO_2 m^{-2} yr^{-1} for period 1 May to 30 September during 2001–2004 reported by Riutta et al., (2007). Pumpanen et al. (2004) report a R value of 1900 g CO_2 m^{-2} yr^{-1}, and Kolari et al. (2006) report an NFFE value 1756 g CO_2 m^{-2} yr^{-1} for the period 20 April to 20 November 2003 for upland an Vitis Idea, VT, Scots pine–Norway spruce forest. These values are comparable to our value of 1124 ± 116 g CO_2 m^{-2} yr^{-1} for upland VT forest station. Also the NEE value from our VT forest of 100 yr (-806 ± 448 g CO_2 m^{-2} yr^{-1}) corresponds well to the value of -1184 g CO_2 m^{-2} yr^{-1} for a VT Scots pine–Norway spruce forest of 75 yr reported by Kolari et al. (2004).

Several studies have shown that ecosystem respiration is dominated by the CO_2 efflux from soil (Valentini et al., 2000; Janssens et al., 2001; Kolari et al., 2004). However, the soil carbon efflux seems to follow a different seasonal pattern from that of total

Table 4. Annual mean values (± standard deviation) of forest floor respiration efflux (R), forest floor vegetation photosynthetic uptake (P), net forest floor exchange (NFFE), net primary production of trees (NPPt), autotrophic respiration of trees (Ra), respiration of tree roots (Rtr) ±25% deviation, ecosystem gross photosynthetic production (GPP), ecosystem gross respiration (GR), net ecosystem exchange (NEE) ±sum of all deviations, all in $gCO_2\ m^{-2}\ yr^{-1}$. Minus sign for CO_2 uptake. Ratios of R/GR and P/GPP in%. (See Table 1 for forest type acronyms). * Carbon use efficiency (CUE) (Spruce 0.292, Pine 0.338, Birch 0.461), and Rtr/Ra ratio (Spruce 0.625, Pine 0.698, Birch 0.65) values are according to Ryan et al., (1997)

CO_2 exchange	Station (and site type)								
Component	1(CT)	2(VT)	3(MT)	4(OMT)	5(OMT+)	6(KgK)	7(KR)	8(VSR1)	9(VSR2)
R	2401	1549	1653	2813	1852	2010	1951	1263	1605
	±469	±126	±109	±403	±230	±420	±448	±268	±315
P	−858	−425	−384	−307	−548	−371	−796	−1168	−1632
	±247	±44	±27	±83	±88	±72	±90	±113	±109
NFFE	1543	1124	1269	2507	1304	1639	1155	95	−256
	±361	±116	±102	±321	±233	±483	±382	±277	±208
NPPt	−420	−812	−1216	−1761	−865	−697	−376	−154	−49
Ra = NPPt/CUE* -NPPt	825	1597	2392	3464	1701	1372	740	303	97
Rtr from Rtr/Ra ratio*	578	1118	1674	2425	1191	960	518	212	68
	±145	±280	±419	±607	±298	±241	±130	±54	±17
GPP = NPPt - Ra + P	−2102	−2834	−3992	−5532	−3114	−2440	−1912	−1625	−1778
GR = R + Ra - Rtr	2648	2028	2370	3853	2362	2421	2173	1354	1634
NEE = NPPt - Rtr + R + P	546	−806	−1621	−1679	−752	−19	261	−271	−373
	±860	±448	±554	±1091	±616	±732	±667	±433	±440
R/GR	91%	76%	70%	73%	78%	83%	90%	93%	98%
P/GPP	41%	15%	10%	6%	18%	15%	42%	72%	92%

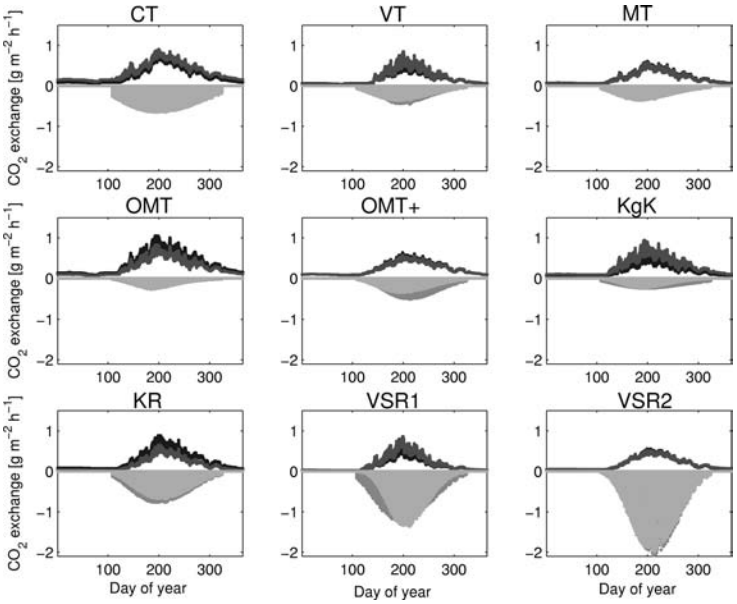

Fig. 7. Integrated 30 min forest floor CO_2 emissions to atmosphere (respiration R), and CO_2 uptakes from atmosphere (photosynthesis P, minus sign) [g m^{-2} h^{-1}]; for individual study plots of nine forests (CT, VT, MT, OMT, OMT+, KgK, KR and two VSR sites; for forest type acronyms, see Table 1). *high density of points in figure overlap into areas

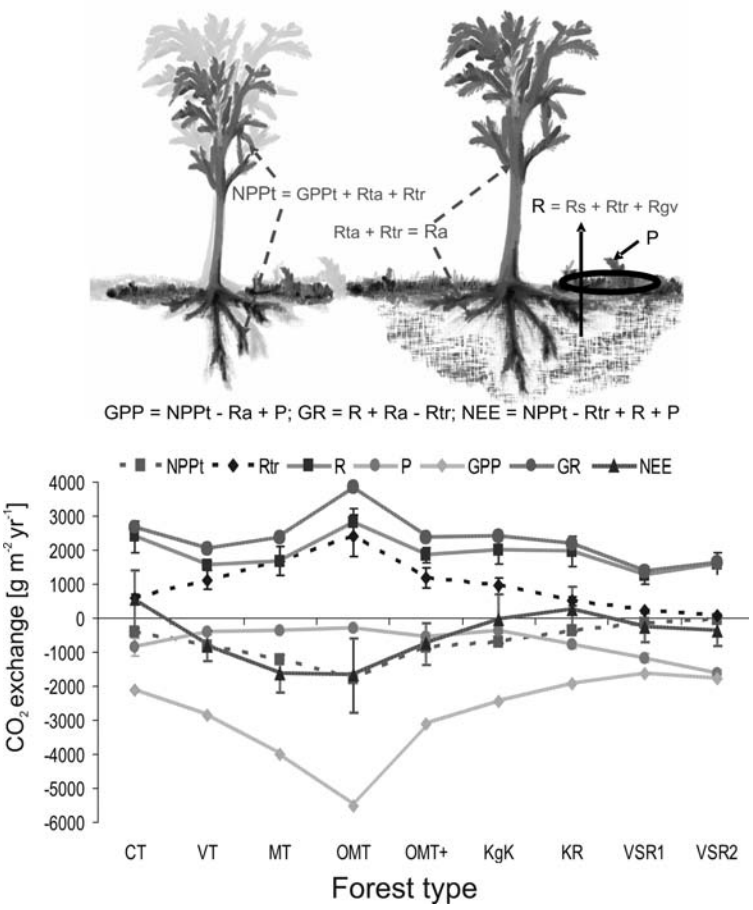

Fig. 8. Schematic of CO_2 exchange [g m^{-2} yr^{-1}] components and relationship to the studied forest-mire ecotone; annual net ecosystem CO_2 exchange (NEE) of nine different forest types; CO_2 emissions to atmosphere – gross respiration of ecosystem (GR), trees (Ra) including parts above-ground (Rta) and tree roots (Rtr), forest floor (R) including forest soil autotrophic (ground vegetation (Rgv) and Rtr and heterotrophic part (Rs); CO_2 uptake from atmosphere – gross photosynthesis of ecosystem (GPP, negative values), forest floor plants (P, negative values) and net photosynthetic production of trees (NPPt, negative values) including tree gross photosynthetic production (GPPt, negative values), Rta and Rtr. The Rtr value is a proportion of Ra and calculated from NPPt and carbon use efficiency (CUE) according to Ryan et al. (1997) after adapting to similar ecosystem and climate conditions (for Ra equation, CUE values and Rtr/Ra ratios, see Table 4). Error bars for R and P values represent standard deviation of three forest type plots, for Rtr values 25% of estimate, and for NEE values the sum of all (no error estimation for NPPt values). For forest type acronyms, see Table 1.

ecosystem respiration. Davidson et al. (2006) found a distinct seasonal pattern in the ratio between soil respiration and total ecosystem respiration, with a clear minimum in spring. Kolari et al. (2006) found that 13% of the annual GPP in an upland pine dominated forest was fixed by ground vegetation. FF photosynhtesis values observed in our study contributed from 6% to 41% to GPP for upland mineral forests, from 15% to 18% for forest-mire transitions, and 42% to 92% for peatlands with

sparse trees. In sparsely forested peatlands, the proportion of carbon uptake by ground vegetation is so high that the role of the trees is usually neglected (Alm et al., 1997; Nykänen et al., 2003). However, the total carbon stores of forested peatlands will increase if WT level would be lowered and forest growth increased (Laine and Minkkinen, 1996).

The largest differences in FF respiration between the forest types due to soil temperature mainly occur during spring (Aurela et al., 2004). Also during summer large differences in R-values between upland and peatland forest types can occur. For example, during hot periods when high FF respiration rates occur in peatlands with lowered WT levels (Alm et al., 1999). However, in our study the annual soil temperature differences between the forest types did not correspond to their differences in annual respiration. The FF CO_2 effluxes did, however, correlate with stand foliar biomass. Janssens et al. (2001) and Högberg et al. (2001) claimed that most soil CO_2 emissions come from rather recently photosynthesized assimilates. Thus, instead of differences in annual temperature, it is the differences in tree photosynthesis and tree root respiration that mainly governs FF and total ecosystem respiration of treed sites. For the upland sites, the highest standing stock and foliage biomass was associated with the Spruce dominated *Oxalis-Myrtillus*, OMT, station, which also had the highest annual respiration value. The second highest soil CO_2 efflux value was associated with least fertile pine dominated *Calluna*, CT, station but which had the highest upland FF photosynthesis. It is possible that the upland respiration values reflected variation in fine root biomass along the mesic gradient, and that high FF respiration corresponds to high fine root biomass of trees and FF plants. The ratio of tree fine root biomass to foliage biomass tends to increases from fertile to less fertile conditions (Vanninen and Mäkelä, 1999), and pine tends to have more roots per leaf area than spruce (Chen et al., 2004). The pine dominated CT station had almost four times more above-ground FF biomass than the spruce dominated OMT station. The above-ground FF biomass was most strongly correlated to FF photosynthesis, and therefore P also increased enhanced R.

The net FF CO_2 exchange in the forest-mire transition zone was at similar level to that of the upland forests. The NFFE of the less stocked transition (*Oxalis-Myrtillus Paludified*, OMT+ and *Myrtillus Spruce Forest Paludified*, KgK) sites indicated that the importance of the respiration of the peat was contributing more to R than the respiration of the tree fine root biomass, while P was still limited by the tree canopy light reduction. The NFFE values of peatlands with only sparse trees showed a balanced C budget. However, the net CO_2 exchange at the FF is only a part of the net ecosystem exchange. When the CO_2 exchange of the above-ground part of the tree stands was included, most of our forested sites acted as carbon sinks, as reported in other studies (Valentini et al., 2000; Kolari et al., 2004; Liski et al., 2006). However, the least forested peatland site the *Tall Sedge Pine Fen*, VSR, remained a net CO_2 sink, and the forest-mire transition and *Spruce Pine Swamp*, KR, sites were balanced.

6. Conclusions

FF CO_2 uptake was most strongly related to the above-ground biomass of the FF, and solar radiation received, which are both strongly determined by the tree canopy. FF CO_2 emission therefore correlated to the tree stand foliar biomass. Whole net ecosystem CO_2 exchange was related to the amount of spruce and pine biomass. The proportion of FF CO_2 exchange in ecosystem CO_2 exchange generally increased as the tree stand became sparser. The net ecosystem exchange of the forest-mire transition zone was balanced because FF light, soil moisture and temperature conditions are so dynamic in this zone, it can fluctuate between being a carbon sink or source. Therefore, for landscape level CO_2 exchange assessment, the dynamics of forest-mire transitional zone, although narrow, is particularly important and in need of further study.

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