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Net CO_2 exchange rates in three different successional stages of the "Dark Taiga" of central Siberia

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ABSTRACT

The net ecosystem exchange (NEE) of successional stages of the *Abies*-dominated dark taiga was measured in central Siberia (61°N 90°E) during the growing season of the year 2000 using the eddy covariance technique. Measurements started before snow melt and canopy activity in spring on day of year (DOY) 99 and lasted until a permanent snow cover had developed and respiration had ceased in autumn DOY 299. Three stands growing in close vicinity were investigated: 50 yr-old *Betula pubescens* ("Betula stand", an early successional stage after fire), 250 yr-old mixed boreal forest, representing the transition from *Betula*-dominated to *Abies*-dominated canopies, and 200-yr-old *Abies sibirica* ("Abies stand", representing a late successional stage following the mixed boreal forest). The mixed boreal forest had a multi-layered canopy with dense understory and trees of variable height and age below the main canopy, which was dominated by *Abies sibirica*, *Picea obovata* and few old *Betula pubescens* and *Populus tremula* trees. The Abies stand had a uniform canopy dominated by *Abies sibirica*. This stand appears to have established not after fire but after wind break or insect damage in a later successional stage. The stands differed with respect to the number of days with net CO_2 uptake (Betula stand 89 days, mixed boreal forest 109 days, and Abies stand 135 days), maximum measured LAI (Betula 2.6 m^2 m^{-2}, mixed boreal forest 3.5 m^2 m^{-2} and Abies stand 4.1 m^2 m^{-2}) and basal area (Betula stand 30.2 m^2 ha^{-1}, mixed boreal forest 35.7 m^2 ha^{-1}, and Abies stand 46.5 m^2 ha^{-1}). In the mixed boreal forest, many days with net daytime CO_2 release were observed in summer. Both other sites were almost permanent sinks in summer. Mean daytime CO_2 exchange rates in July were -8.45 μmol m^{-2} s^{-1} in the Betula stand, -4.65 μmol m^{-2} s^{-1} in the mixed boreal forest and -6.31 μmol m^{-2} s^{-1} in the Abies stand. Measured uptake for the growing season was -247.2 g C m^{-2} in the Betula stand, -99.7 g C m^{-2} in the mixed boreal forest and -269.9 g C m^{-2} in the Abies stand. The total annual carbon uptake might be slightly lower (i.e. less negative) due to some soil respiration under snow in winter. The study for the first time demonstrates that old forests in the "Dark Taiga" are carbon sinks and that sink activity is very similar in late and early successional stages. Canopy and crown structure with associated self-shading and available radiation are suggested as possible causes for the observed differences.

1. Introduction

There is a growing need not only to study net ecosystem exchange (NEE) rates of the main vegetation types but also to understand the observed variability of NEE in different global vegetation types in order to quantify a global carbon balance (Valentini et al., 2000; Janssens et al., 2001; Jarvis et al., 2001). In the past, the boreal forest has mainly been studied in Canada and Scandinavia (Baldocchi et al., 1997; Jarvis et al., 1997; Lavigne and Ryan, 1997; Lavigne et al., 1997;

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Lindroth et al., 1998; Baldocchi et al., 2000), whereas the Siberian boreal region, which contributes 20% of the global boreal region, has been underrepresented. The fire-prone forests of *Pinus sylvestris* of western Siberia (Kelliher et al., 1998; Shibistova et al., 2002) and of eastern Siberian *Larix* (Hollinger et al., 1998) have been investigated, but the "Dark Taiga", which is dominated by *Abies* and *Picea* and which has a very low fire frequency (Mollicone et al., 2002), has not been studied so far. These forests appear to be the most productive ecosystems in boreal Siberia (Gower et al., 2001), mainly because of fertile soils and less disturbance by fire. However, this forest type grows in a diverse landscape in which different successional stages occur together on a very close geographic scale due to the effects of natural disturbances.

In the following we investigate the net ecosystem exchange of the most representative stages of the fire succession in the "Dark Taiga": the *Betula* stage, the mixed *Abies*/*Picea* boreal forest, and the *Abies* forest. The investigated stands grew in close geographic vicinity on the same soil, in the same climate and with similar exposition. Thus we investigate how structural and species composition affect the carbon balance in consecutive successional stages. It will be shown that the old forests are carbon sinks, that early and late successional stages are carbon sinks of very similar magnitude, and that stand structure and associated self-shading is a key factor for the carbon balance in northern latitudes.

2. Material and methods

2.1. Site characteristics

Measurements were made in three stands of boreal forest in central Siberia representing different successional stages after fire. The study area is located 10 km east of the river Yenisey, opposite the settlement Vorogovo (61°01′N, 89°34′E). Measurements took place from DOY 99 (early April 2000 before snow melt) until DOY 299 (late October after permanent snow cover on forest floor). The stands were located on a plateau which forms the initial rise of the Central Siberian Mountain Range on the east bank of the Yenisey river. The maximum distance between two stands was 2.7 km; the closest two stands were 940 m apart. Soils were cambisols on sandy silt (Wirth and Czimczik, personal communication), with larger tree roots growing in the upper layer of the soil and fine roots reaching a depth of 60 cm. The tower sites were located between 180 and 200 m a.s.l.

The vegetation is classified as "Dark Taiga", which is a moist boreal forest dominated by *Abies* and *Picea* in later succession, contrasting the "Light Taiga" dominated by *Pinus* and *Larix* on drier and fire-prone habitats. The "Dark Taiga" is characterized by a fire cycle of almost 400 yr (Mollicone et al., 2002). Fire succession starts with *Betula pubescens*, which is in some cases mixed with *Populus tremula* depending on drainage conditions. The coniferous species germinate simultaneously but are initially suppressed by the deciduous species. Being shade tolerant, however, the conifers eventually grow through the *Betula* canopy and, due to their longevity, replace it after about 100–150 yr. In this period of transition, a mixed boreal forest exists in which aging *Betula* and tall *Picea* and *Abies* trees dominate a canopy that has a second and third tree layer of mainly conifers. About 200–400 yr after fire, a mixed coniferous forest exists. *Abies* is very shade tolerant and dominates the understory. It is also the fastest growing species when light becomes available after disturbance other than fire (i.e. by insects, snow break or wind). In such cases, *Abies* forms almost even-aged mono-cultures with uniform canopies, resembling the "pole" stage in managed forest systems. *Picea* and *Pinus sibirica* still persist because they germinate on dead logs. The cycle of non-fire disturbance may continue for several hundred years over several forest generations before being interrupted by fire again.

This study is based on three characteristic stages in this long-term fire succession: (1) a 50 yr-old *Betula* stand established after fire with small amounts of poplar and a few patches of fir and spruce re-growth, (2) a mixed boreal forest in which the canopy is dominated by about 250 yr-old tall *Abies* and *Picea* trees and in which a few old *Betula* trees persist, and (3) a "pole" stand of ca. 200 yr-old *Abies*. In the following we will refer to these stands as (1) "Betula stand", (2) "mixed boreal forest" and (3) "Abies stand" (Table 1). The mixed boreal forest site tower was identical to that used by Styles et al. (2002).

The Betula stand was a mono-culture of even-aged stems of *Betula pubescens* (Table 2). The stand contained some patches of *Populus tremula*, and a few small conifers representing the first coniferous generation coming up after the fire. The mixed boreal forest had an upper canopy layer formed by *Abies sibirica*, *Picea obovata* and *Pinus sibirica* mixed with few old stems of *Betula pubescens* and *Populus tremula*.

Table 1. *Geographical, geological and forest stand structure related site characteristics of the three measurement site*

Site	Betula	Mixed	Abies
Location	61° 01′ 57″N 89° 49′ 10″E	61° 01′ 49″N 89° 47′ 13″E	61° 01′ 52″N 89° 46′ 11″E
Elevation (m a.s.l.)	200	180	180
Soil type	Cambisol	Cambisol	Cambisol
Stand age (yr)	50	250	200
Canopy structure	Even-aged	Uneven-aged	Transition stage
Main canopy height (m)	15	22	22
Dominating genus	*Betula*	*Abies*	*Abies*
Stand density (trees ha^{-1})	4600	2467	1056
Basal area (m^2 ha^{-1})	30.2	35.7	46.5

Table 2. *Species compositions (%) of the three stands given as species abundancies in percent of total number of trees per stand*

	Abies	*Picea*	*Pinus*	*Betula*	*Populus*	*Sorbus*
Betula	4	-	-	67	1	27
Mixed	57	14	7	6	-	17
Abies	71	6	3	1	-	20

This forest was characterized by several tree layers in the sub-canopy (4–18 m) formed by conifers only. A fairly dense understory (<4 m) was formed by conifers and shrubs of *Sorbus aucuparia*. There was a species-rich herbaceous layer. This contrasted the Abies stand, which had only one main canopy and ground vegetation composed mainly of *Vaccinium*. Understory existed on small gaps caused by snow break.

Distribution of stem diameter at breast height (DBH), which is used as a proxy for tree height distribution, showed only few diameter classes in the Betula stand – the typical even-aged growth pattern of young stands (Fig. 1). In the mixed boreal forest, the DBH distribution showed a smooth, exponentially declining curve typical of old-growth, uneven-aged stands. The smallest diameter class (counting only trees of a height above 1.3 m) contributed 40% of the total number. In the Abies stand, the smallest trees accounted for 25% of the total number and were clumped on gaps of fallen or broken tree individuals. There was a larger fraction of medium-sized trees which formed the main canopy. Few large trees represented the former tree generation. The two coniferous stands also differed in their basal area: Fig. 2 shows that total basal area of 46.5 m^2 ha^{-1} in the Abies stand was 1.3 times that of the mixed boreal forest, the relative portions of the single species being similar for both stands. Thus, the mixed boreal forest had a very different stand structure, with many more small trees and fewer tall trees than the Abies stand.

2.2. Eddy correlation measurements

The measurements started in early April 2000 when the winter snow cover of more than 1 m had not yet melted, and ended in October 2000 when the organic layer was frozen and a permanent snow cover had established. At all three sites CO_2, energy and momentum fluxes were measured using an eddy covariance system similar to those used in the Euroflux project (Aubinet et al., 2000), consisting of the following devices: a three-axis sonic anemometer with an omni-directional head (model Solent R3, Gill Instruments, Lymington, UK) and a fast response closed-path CO_2/H_2O non-dispersive infrared gas analyzer (model LI6262, LiCor Inc., Lincoln, NB, USA). Details of the measurement setups are given in Table 3.

The analyzer was run in absolute mode with CO_2 and water-free air circulating in the reference cell and the chopper housing, using a combination of magnesium perchlorate and soda-lime for scrubbing. Calibration of the instrument was checked regularly at least once a week using air of known CO_2 (pressurized bottle) and H_2O (dew-point generator, model LI610, LiCor Inc., Lincoln, NB, USA) concentrations for the span and pure N_2 (pressurized bottle) for the zero setting.

Electric power was supplied by generators charging battery arrays. The generators were situated downwind of the towers with respect to main wind direction in

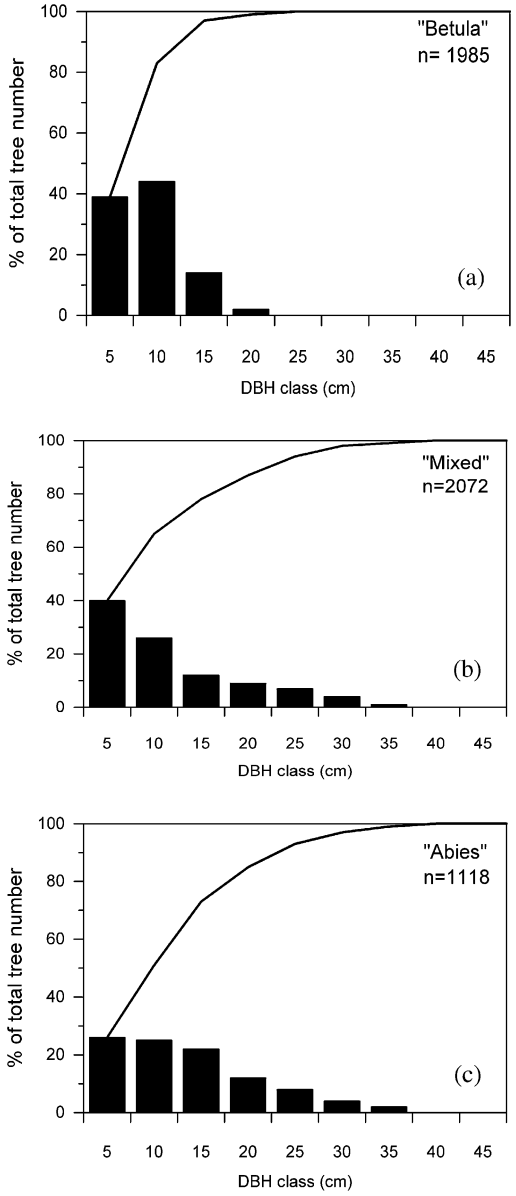

Fig. 1. Distributions of diameter at breast height (bars) of living trees in 5 cm classes for the Betula stand (a), the mixed boreal forest (b) and the Abies stand (c). The lines indicate the cumulative percentage of trees over DBH classes.

order to avoid an influence of the exhaust fumes on the measurements for most of the time. The distance between the tower and the generator was approximately 200 m at the mixed boreal forest and the Betula stand and 800 m at the Abies stand.

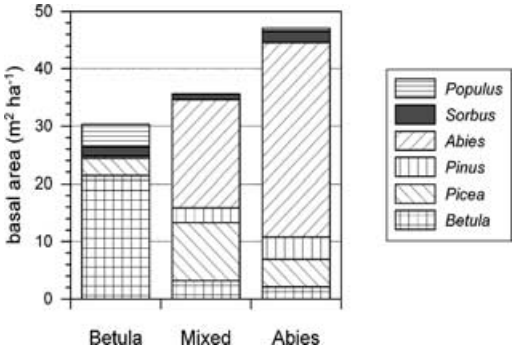

Fig. 2. Basal areas of the individual species in the Betula stand, in the mixed boreal forest and in the Abies stand.

On-line calculation of sensible heat and latent heat fluxes and NEE were performed using the EDDYMEAS software developed by Olaf Kolle (Max Planck Institute for Biogeochemistry, Jena, Germany). Final flux calculations included coordinate-rotation as described in McMillen (1988). Time lags between measurements of w' (deviation of the vertical wind velocity via the sonic) and x' (deviation of the concentration values via the gas analyzer) were calculated individually for each half hour run by finding the highest cross-correlation. Associated with the use of closed-path analyzers are flux losses attributable to the incomplete spectral response of the analyzer, to frequency depending dampening of the signal along air flow through the tube, and to the separation between the tube inlet and the sonic anemometer head. These were accounted for by comparing normalized co-spectra of vertical wind velocity and temperature to co-spectra of vertical wind velocity and measured concentrations of CO_2 and H_2O, respectively. The temperature co-spectra represent the entire turbulent sensible heat flux density without losses: no signal dampening, no sensor separation, sufficient frequency response. In particular, they are defined by a linear function with a slope of $-4/3$ in the inertial, high frequency subrange, whereas co-spectra for CO_2 or H_2O show a steeper decline due to the flux losses mentioned above. Applying an inductance factor according to Eugster and Senn (1995) aligned the graphs with that of the temperature co-spectrum.

There were only minor differences in calculated time lags and inductances between the three sites: time lags varied from 3.85 (Abies stand) to 4.93 (Betula stand) for CO_2, and from 4.35 (Abies stand) to 4.98 (Betula stand) for H_2O. Inductances were 0.1 (mixed

Table 3. *Technical characteristics of the eddy correlation measurement setups at the three sites in the mixed boreal forest, the Abies and the Betula stand*

	Betula	Mixed	Abies
Type of tower	120 cm × 250 cm (scaffolding)	30 cm × 30 cm (aluminium)	30 cm × 30 cm (aluminium)
Measurement height (m)	22.0	28.7	26.3
Type of tubing (diameter)	DEKABON (4 mm)	BEV-A-Line (1/8″)	BEV-A-Line (1/8″)
Pump	Diaphragm (pushing), KNF Neuberger, Germany	Diaphragm (pushing), KNF Neuberger, Germany	Diaphragm (pushing), KNF Neuberger, Germany
Flow rate (L min^{-1})	7.0	6.5	7.0

Table 4. *Technical characteristics and sensor types of the meteorological measurement setups at the three sites*

Quantity	Betula	Mixed	Abies
Total up- & downwards radiation		Pyrradiometer LXG055, Dr. Lange, Berlin, Germany	Pyrradiometer LXG055, Dr. Lange, Berlin, Germany
Short-wave up- & downwards radiation		Albedometer CM14, Kipp and Zonen, Delft, Netherlands	
Photon flux density	LI-190SA, LI-COR, Lincoln, USA	LI-190SA, LI-COR, Lincoln, USA	
Net radiation	Net radiometer (Middleton, Australia		
Air temperature & humidity	HMP45D, Vaisala, Helsinki, Finland	HMP45D, Vaisala, Helsinki, Finland	
Air pressure		Pressure transducer PTB101B, Vaisala, Helsinki, Finland	
Wind velocity		Cup anemometer A100R, Vector Instruments, Rhyl, Clwyd, United Kingdom	
Wind direction		Wind vane W200P, Vector Instruments, Rhyl, Clwyd, United Kingdom	
Rain	Rain gauge 2203, R.M. Young Company, Traverse City, Michigan, USA	Rain gauge 2203, R.M. Young Company, Traverse City, Michigan, USA	
Soil heat flux	Heat flux plates REBS, Radiation and Energy Balance Systems, Inc. Seattle, WA (U.S.A)	Heat flux plates RIMCO HP3/ CN3, McVan Instruments, Mulgrave, Victoria, Australia	Heat flux plates RIMCO HP3/ CN3, McVan Instruments, Mulgrave, Victoria, Australia
Soil temperature	Platinum resistance thermometers with PT100 glass resistors (Geratherm, Geschwenda, Germany)	Platinum resistance thermometers with PT100 glass resistors (Geratherm, Geschwenda, Germany)	Platinum resistance thermometers with PT100 glass resistors (Geratherm, Geschwenda, Germany)
Soil moisture		FDR probe ML2x, Delta-T Devices, Burwell, Cambridge, United Kingdom	FDR probe ML2x, Delta-T Devices, Burwell, Cambridge, United Kingdom

boreal forest, Betula stand) and 0.2 (Abies stand) for CO_2 and 0.2 (mixed boreal forest, Betula stand) and 0.3 (Abies stand) for H_2O. This shows that the experimental design aiming at comparable measurements succeeded in obtaining similar characteristics for the set-ups in all the three sites.

2.3. Meteorological and LAI measurements

The towers were equipped with a number of instruments to measure environmental variables (see Table 4 for instrument types at all the three sites). In the mixed boreal forest, radiative flux measurements included total downward and upward radiation using a

pyrradiometer, short-wave downward and upward radiation using an albedometer, and photon flux density. Net radiation was calculated using both the pyrradiometer and the albedometer to account for different sensitivities of the pyrradiometer in short- (solar) and long- (terrestrial) wave radiation range. Additional measurements included air temperature and air humidity, air pressure, wind velocity and wind direction. These sensors were installed below the sonic anemometer on a boom. On ground level (below the canopy) a rain gauge was set up close to the eddy flux tower.

The tower at the Abies stand was equipped with a pyrradiometer only, where net radiation was calculated as difference of total downward minus total upward radiation. Long- and short-wave sensitivities were averaged in this case.

At both the mixed boreal forest and the Abies stand, soil heat flux was measured at five locations with heat flux plates installed at a depth of 0.05 m. For measurement of soil temperatures, home-made platinum resistance thermometers on 1 cm diameter rods were installed at depths of 0.05 m, 0.15 m, 0.50 m and 1.0 m, respectively. Soil moisture was measured with a TDR probe at a depth of 10 cm at both sites. The environmental data were collected every 10 s and stored as 10 min averages on data loggers (model CR23X, Campbell Scientific, Shepshed, Leicestershire, UK).

The tower in the Betula stand was equipped with a net radiometer, a photon flux density sensor, a rain gauge, and an air temperature-humidity sensor. Sensors installed below the canopy layer and in the soil included two soil heat flux plates at a depth of 0.05 m, and five soil temperature sensors placed at a depth of -0.05, -0.1, -0.25, -0.50 and -1.0 m. All data were collected every 10 s and stored as 30 min averages on a data logger (model CR10, Campbell Scientific, Shepshed, Leicestershire, UK).

Leaf area index (LAI) was measured regularly at all three sites with a Li-Cor LAI 2000 canopy analyzer. For the Abies stand and the mixed boreal forest, values measured in April were multiplied by a factor of 1.6 as opposed to the factor of 1.4 for the remaining measurement period because of the lack of broad-leaved effects so early in the year.

2.4. Data quality and energy balance closure

Data gaps in CO_2-flux measurements of more than 2 h due to system or electric power failures, calibration or maintenance comprised 20.1% of all measured data in the Abies stand, 8.4% in the mixed boreal forest and 16.8% in the Betula stand. A major gap with total data loss in the mixed boreal forest and the Abies stand occurred on 20–24 June due to power failure. These gaps were filled by modeling the missing fluxes from weather data (see below).

Data quality in all three stands was assessed by looking at stationarity tests, integral turbulence characteristics, vertical wind speed class distribution, footprint analyses, and energy balance closures. However, no thresholds for the corresponding parameters were defined for any exclusion of extreme values when calculating net ecosystem exchanges of CO_2. The quality indicators were rather used to assess the overall quality of the sites regarding the applicability of the eddy correlation methodology. The Abies stand showed an overall better data quality than the mixed boreal forest, having lower percentages of non-stationary conditions and better defined footprints. The energy balance closures were of 89.6% at the Abies stand, of 80.4% in the mixed boreal forest and of 80.1% in the Betula stand (Fig. 3), but all three sites were found to show satisfactory data quality for reliable measurements.

For calculating the energy balance closure, daytime sums of sensible and latent heat fluxes were plotted against total available radiation energy minus ground heat flux and storage terms as defined by Knohl (1999). Daytime in this study was defined as the period of the day with PAR measured above the canopy above 30 μmol quanta m^{-2} s^{-1}.

The co-spectra of temperature and wind velocity showed the typical curve with a linear decline of ca. $-4/3$ slope in the high frequencies (an example is given in Fig. 4). This accordance with the theoretical shape of the curve is an indication of good general conditions for eddy co-variance measurements.

2.5. Treatment of nighttime values and data gaps

In order to avoid an underestimation of nighttime respiration that occurs because of CO_2 storage under non-convective conditions, data points obtained under conditions with a friction velocity u^* below a threshold value were rejected (Jarvis et al., 1997). All three stands showed moderately growing values of NEE with increasing friction velocity. $u^* = 0.2$ m s^{-1} was chosen as a threshold for all three sites, as suggested by Aubinet et al. (2000) and Barford et al. (2001). The rejected values were then replaced by modeling respiration in dependence of soil temperature with an Arrhenius formula modified according to

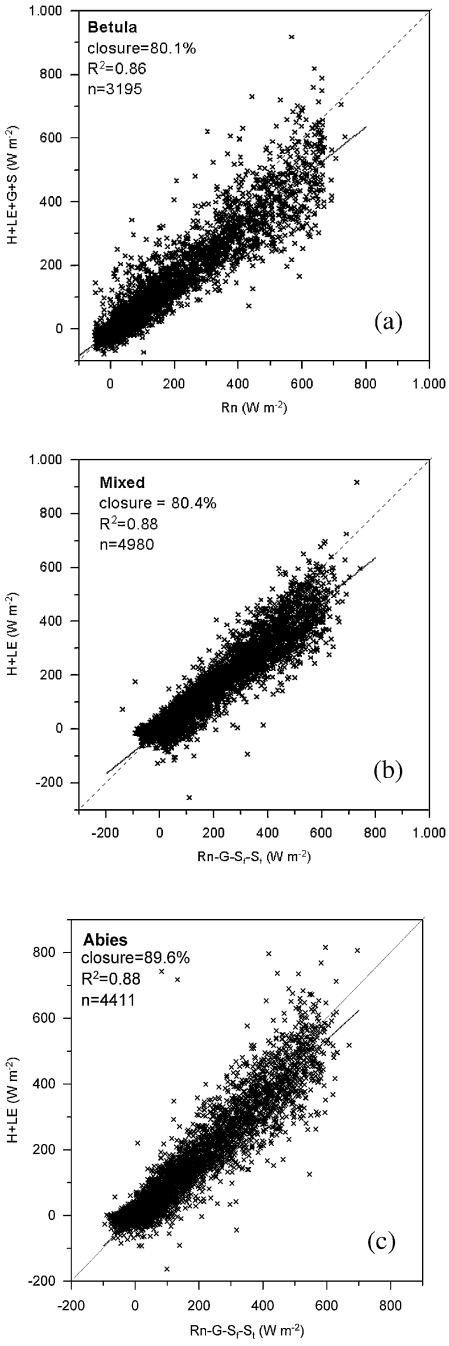

Fig. 3. Energy balance closures in the Betula stand (a), the mixed boreal forest (b) and the Abies stand (c) evaluated from daytime half-hourly values (PAR $\leq$ 30 μmol quanta m^{-2} s^{-1}).

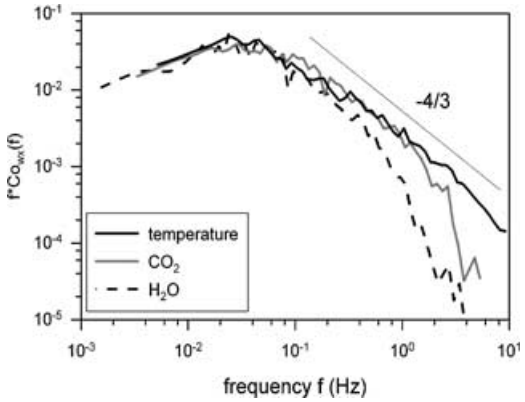

Fig. 4. Co-spectra of vertical wind (w) with temperature (solid black line), CO_2 (solid grey line) and H_2O (dashed black line) for 28 June 2000 (9:00–15:00) in the Abies stand. The co-spectral densities are multiplied by the frequency (f). As expected according to the theory of Eugster and Senn, (1995), the graph of the temperature co-spectrum shows a $-4/3$ slope for the high-frequency range, whereas the co-spectra for CO_2 and H_2O decline more steeply without correction by inductance.

Lloyd and Taylor (1994). This equation was also used to fill night-time gaps in the data sets caused by instrument or power failure.

Daytime gaps during the growing season were filled by modeling NEE in dependence of photosynthetic photon flux density (PPFD) using the modified Michaelis–Menten equation

$$F_C = -[(a\mathrm{PPFD}b)/(a\mathrm{PPFD} + b) - c].$$

The parameters a, b and c were calculated separately for every 20 days.

3. Results and discussion

3.1. Climatic conditions

During the measurement period the temperature of the air ranged between $-17.2\,^{\circ}$C (October) and $35.0\,^{\circ}$C (June). The frost-free period lasted 134 days. Rainy precipitation was well distributed across seasons, the snow period started in October. Soil water content dropped below a volumetric content of 20% only during a few days in July.

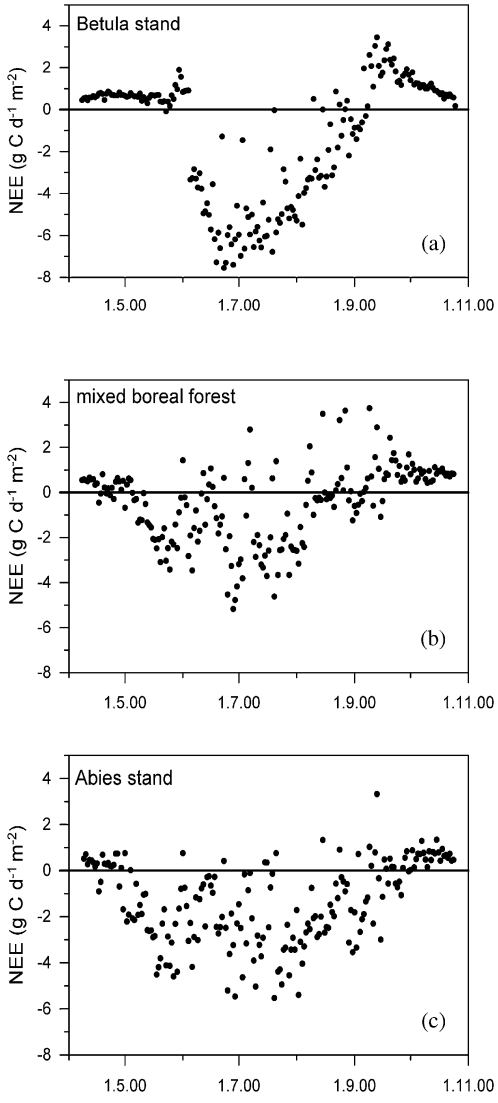

Fig. 5. Annual courses of daily NEE of CO_2 in the Betula stand (a), the mixed boreal forest (b) and the Abies stand (c).

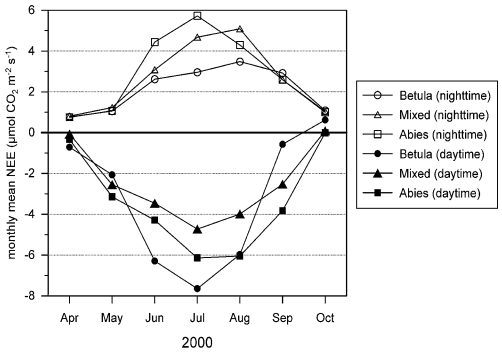

Fig. 6. Comparison of monthly averages of daytime and night-time net CO_2 exchange rates in the Betula stand (open and solid circles), the mixed stand (opens and solid triangles) and the Abies stand (open and solid squares). Night-time is defined as that period of the day with PAR <30 μmol quanta m^{-2} s^{-1}.

3.2. *CO_2 flux measurements*

Daily (24 h) net ecosystem exchange rates of CO_2 showed an annual course with respiration in spring and autumn and net CO_2 uptake in summer for all sites (Fig. 5). In the Betula stand net flux rates increased with leaf expansion in early June. An average maximum sink of -8 g C m^{-2} d^{-1} was reached at the end of June. Despite varying weather conditions, there was no daily net respiration between June and late August. The seasonal course was different in the coniferous stands. Both stands exhibited days with daily net CO_2 uptake during a period that started earlier and ended later than in the Betula stand (May – October), but in both stands there were days with positive NEE also in summer, especially in the mixed boreal forest. The number of days with negative daily CO_2 flux (the stand being a sink) was 89 for the Betula stand, 109 for the mixed boreal forest, and 135 for the Abies stand during the whole measurement period. Maximum rates in the coniferous stands were not as high as in the broad-leafed stand.

Partitioning monthly averages of the net daily exchange rates into night-time fluxes (i.e. respiration) and daytime fluxes (i.e. mostly assimilation, Fig. 6) showed lower respiration rates for the Betula stand as compared to the coniferous sites. Assimilation in the Betula stand started low in May, when the leaves of the birch were not yet developed, but reached higher rates than the coniferous stands in June and July. The autumn decline of assimilation occurred earlier than in the other two stands. The two coniferous stands exhibited respiration rates which were quite similar, although the mixed boreal forest had lower respiration rates than the Abies stand in spring and higher rates in autumn. This is consistent with the faster growth of the Abies stand and a higher proportion of root respiration that has a higher sensitivity to temperature than heterotrophic respiration (Boone et al., 1998).

The main difference between the mixed boreal forest and the Abies stand was observed with respect to daytime fluxes which consistently showed higher net

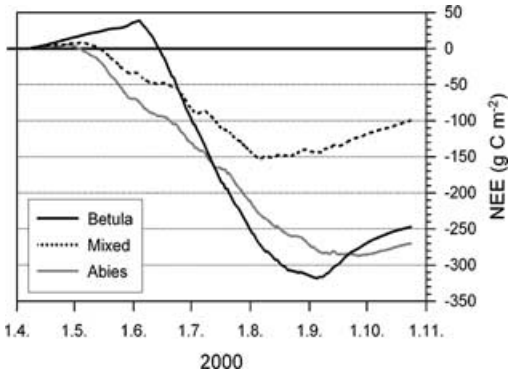

Fig. 7. Cumulative NEE of CO_2 from early April until late October 2000 for the Betula stand (solid black line), the mixed stand (dashed black line), and the Abies stand (solid grey line).

carbon uptakes in the Abies stand than in the mixed boreal forest. Mean daytime CO_2 exchange rates in July were -8.45 μmol m^{-2} s^{-1} in the Betula stand, -4.65 μmol m^{-2} s^{-1} in the mixed boreal forest and -6.31 μmol m^{-2} s^{-1} in the Abies stand (Fig. 6).

The differences in assimilation and respiration determine the cumulative carbon budget. The net carbon uptake between April and November was -247.2 g C m^{-2} for the early successional *Betula* and -269.9 g C m^{-2} for the late successional *Abies* forest, but much lower for the mixed boreal forest (-99.7 g C m^{-2}, Fig. 7). By modeling daytime respiration based on night-time CO_2 fluxes measured at a friction velocity >0.2 m s^{-1} and on soil temperatures measured at a depth of 0.05 m, gross primary production of the three stands over the measurement period could be estimated. Results were 727, 911 and 777 g C m^{-2} for the Betula stand, the Abies stand and the mixed boreal forest, respectively.

This result was unexpected: two stands very different in species composition and successional age but with similar canopy structure showed a similar carbon balance (Betula and Abies stand), and this was in contrast to two stands similar with respect to the dominant species but different with respect to stand structure showing very different carbon balances (Abies stand and mixed boreal forest). In order to interpret this observation, in the following several factors are assessed as potential drivers for the differences in CO_2 exchange, such as leaf area, stand structure and light availability.

Leaf area indices were 20% higher for the Abies stand than for the mixed boreal forest (Table 5). Thus,

Table 5. *Development of leaf area indices (in m^2 m^{-2}) in the three stands over the measurement period*[a]

Period	Betula	Mixed	Abies
April	0.9	2.4	3.0
Early July	2.2	3.0	3.6
Late August	2.6	3.5	4.1

[a]For the Abies stand and the mixed boreal forest, values for April were corrected with a factor of 1.6 as opposed to 1.4 for the other dates because of the lack of broad-leaved effects so early in the year.

part of the response might be due to *Abies* having higher leaf areas than a mixed stand. This difference could, however, be compensated by differences in photosynthetic assimilation between early and late successional species. The Betula and the Abies stand have a very similar annual carbon balance despite very different LAIs. The higher photosynthetic rate of deciduous *Betula* compensating the low leaf area (Schulze,

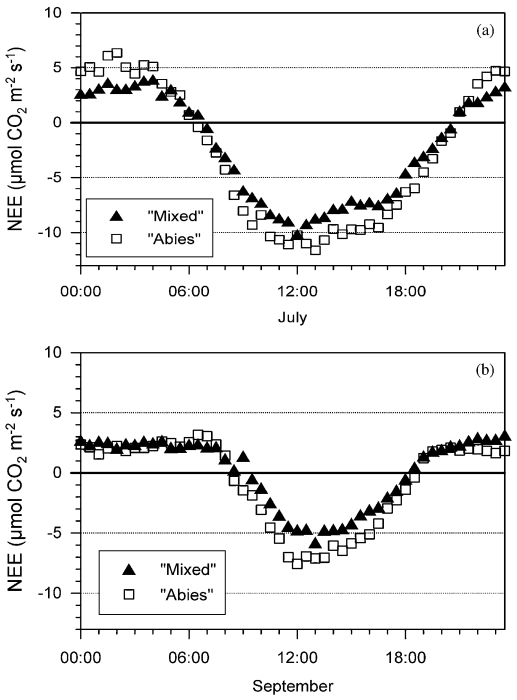

Fig. 8. Average diurnal course of CO_2 NEE in July (a) and September (b) for the mixed boreal forest (solid triangles) and the Abies stand (open squares).

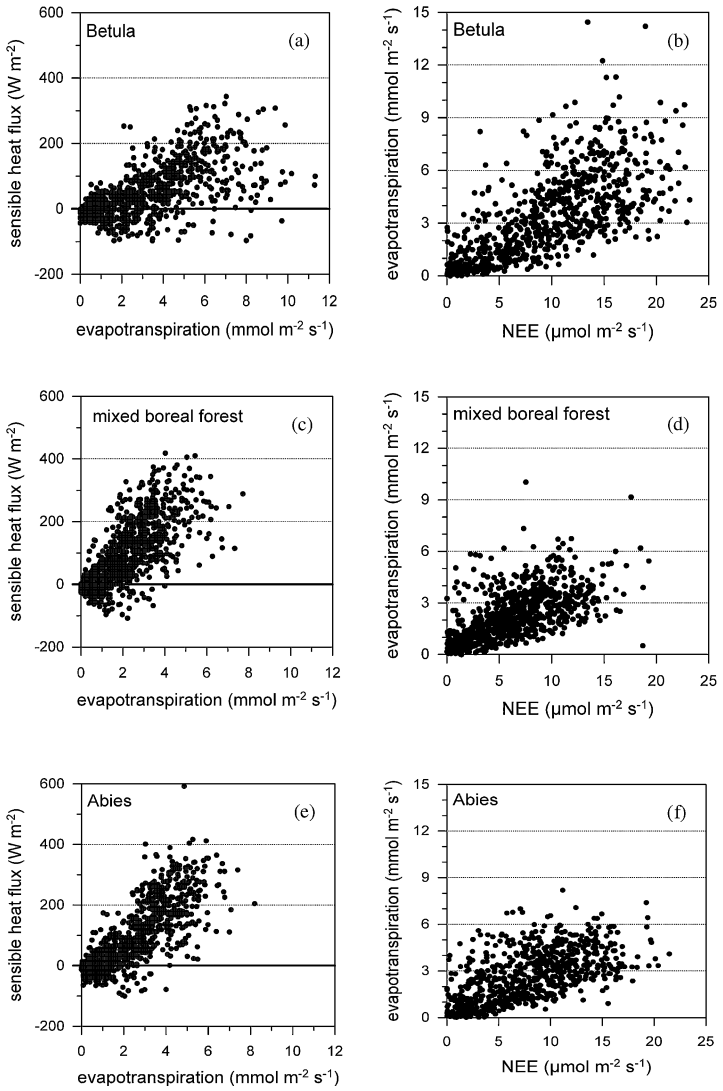

Fig. 9. Relations between sensible heat, evapotranspiration and net ecosystem exchange in July 2000 at the Betula stand (a and b), the mixed boreal forest (c and d), and the Abies stand (e and f). (a, c and e) Relation between evapotranspiration and sensible heat flux. (b, d and f) Relation between NEE and evapotranspiration.

1982) might explain the similar annual carbon balance despite the difference in observed LAI. Similarly, the lower leaf area of the mixed forest, which still contains more *Betula* than the Abies stand, could be balanced by higher average photosynthetic rates per leaf area. Thus, leaf area does not seem to explain the difference in NEE between the two stands.

However, composition and structure must be considered in order to evaluate the efficiency of the existing leaf area. Stand structure was very different between the mixed boreal forest and the Abies stand. In the mixed boreal forest, the few tall specimens of *Picea obovata* shadowed a larger amount of smaller *Abies* with their leaves and boles, especially during mornings and evenings but even at full light due to the location at 60° northern latitude. Self-shading therefore reduced the available light in lower canopy layers, while soil respiration remained unaffected. Investigating

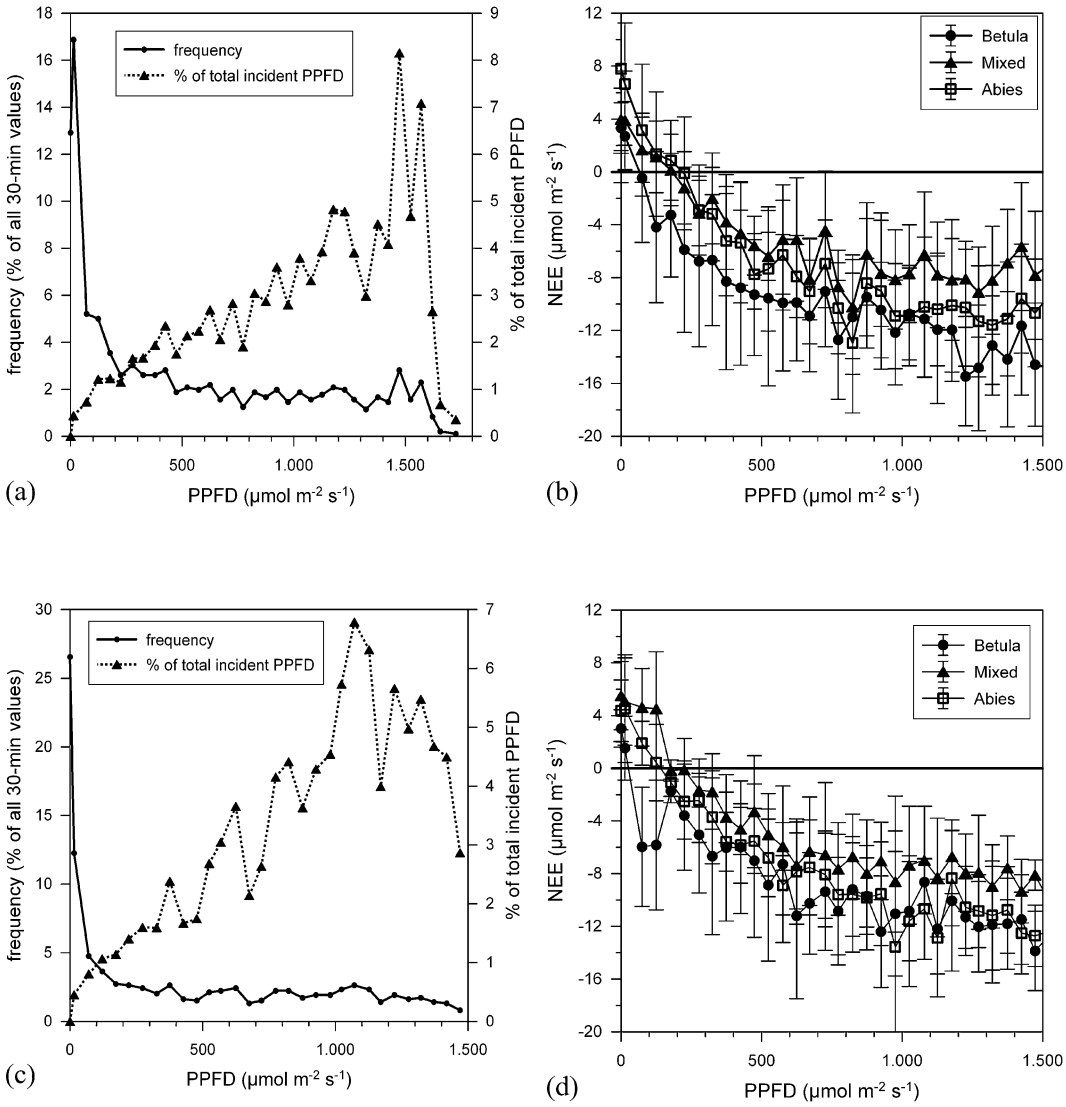

Fig. 10. Distribution of incoming photosynthetically active radiation and average light response curves of NEE at the three stands. (a, b) 17 June–6 July 2000; (c and d) August 2000. In (a) and (c) the frequency distribution of light intensity (as a percentage of all half-hour values) is represented by circles and solid lines, the share that each light intensity has on the total incoming PPFD by triangles and dashed lines. The relation between PPFD and NEE is given in (b) and (d) (Betula stand: triangles, Abies stand: circles, mixed boreal forest: squares). NEE is averaged over bins of 50 μmol quanta m^{-2} s^{-1}; error bars represent standard deviations.

the average daily course of NEE in summer and in autumn (Fig. 8) shows that the effect of dimmed light in the morning and evening does not explain the difference between Abies stand and mixed boreal forest. The effect was strongest at 60° sun angle in summer, which would saturate photosynthesis in the upper canopy, but still cast a lot of shade on the lower canopy in the mixed boreal forest. In September, the effect of dawn and dusk became more clearly apparent in addition to the effect of sun angle at noon. Leaf mass per area and assimilation are both positively correlated with the amount of intercepted radiation,

therefore we can suppose that the differences in leaf mass, and in assimilation, were large between the two stands.

The relation between sensible heat and evapotranspiration during July (Figs. 9a, c and e) was similar for the two coniferous stands, with Bowen ratios ranging around 1. The Betula stand showed lower Bowen ratios. Water-use efficiencies (roughly estimated by regarding the relation between NEE and E) were similar in all three stands, with a slightly lower efficiency in the mixed boreal forest (Figs. 9b, d and f).

An exercise scaling down to leaf level is needed in order to identify the reasons for the observed differences between the assimilation rates of the coniferous forests, and in order to quantify the effects of the main constraints influencing the assimilation, such as nutrients (van Kleve and Vierek, 1981), vapor-pressure deficit and radiation.

However, we suggest that, at 60° of latitude over well watered forests, available radiation can be considered a major constraint on the photosynthesis. The frequency distribution of light intensity showed high values at low light (Figs. 10a and c). The share that each measured intensity had on total incoming PPFD over the regarded period peaked at ca. 1500 μmol quanta m^{-2} s^{-1} at the end of June and at ca. 1100 μmol quanta m^{-2} s^{-1} in August. In order to compare light use efficiencies, we plotted average NEE over PPFD (Figs. 10b and d). This relation showed growing functions for all three stands. Maximum assimilation (A_{max}) was higher for the Abies stand than for the mixed boreal forest, whereas the compensation points of the two stands were similar in both late June and August. The Betula stand showed both a higher degree of saturation at low light intensities and a higher A_{max} than the two coniferous stands. Standard deviations gave an indication about the shape of the envelope curve. These deviations were influenced by other constraints than PPFD, such as vapor-pressure deficit on assimilation or soil temperature on respiration.

Slight differences in slope affecting incident direct radiation can affect available radiation more strongly than at the mid-latitudes (Nobel, 1991). Canopy and crown structures, as leaves distribution and clumping in branchlets (Law et al., 2001), and the associated self-shading can limit the efficiency in light use.

The results show that (1) old forests of the Dark Taiga are carbon sinks, (2) that a late successional forest has the same carbon balance as an early successional forest, and we suggest that (3) in Dark Taiga forests sited at 60° northern latitude, differences in stand structure associated with light availability can cause considerable differences in net ecosystem production.

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