

Carbon balance of a southern taiga spruce stand in European Russia

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ABSTRACT

We present results from nearly three years of net ecosystem flux measurements above a boreal spruce stand growing in European Russia. Fluxes were measured by eddy covariance using conventional techniques. In all years examined (1998–2000), the forest was a significant source of carbon to the atmosphere. However, the magnitude of this inferred source depended upon assumptions regarding the degree of “flux loss” under conditions of low turbulence, such as typically occur at night. When corrections were not made, the forest was calculated to be only a modest source of C to the atmosphere (3–5 mol C m⁻² yr⁻¹). However, when the corrections were included, the apparent source was much larger (20–30 mol C m⁻² yr⁻¹). Using a simple model to describe the temperature dependencies of ecosystem respiration on air and soil temperatures, about 80% of the night-time flux was inferred to be from soil respiration, with the remainder being attributable to foliage, branches and boles. We used reasonable assumptions to estimate the rate of ecosystem respiration during the day, allowing an estimation of canopy photosynthetic rates and hence the annual Gross Primary Productivity of the ecosystem. For the two full years examined (1999 and 2000), this was estimated at 122 and 130 mol C m⁻² yr⁻¹, respectively. This value is similar to estimates for boreal forests in Scandinavia, but substantially higher than has been reported for Canadian or Siberian boreal forests. There was a clear tendency for canopy photosynthetic rates to increase with both light and temperature, but the slope of the temperature response of photosynthesis was less steep than that of ecosystem respiration. Thus, on most warm days in summer the forest was a substantial source of carbon to the atmosphere; with the forest usually being a net sink only on high insolation days where the average daily air temperatures were below about 18 °C. These data, along with other studies on the current balance of boreal ecosystems, suggests that at the current time many boreal forests might be releasing substantial amounts of carbon dioxide to the atmosphere. This observed temperature sensitivity of this ecosystem suggests that this might be a consequence of substantially higher than average temperatures over recent years.

1. Introduction

The role of boreal forests in the global carbon balance, past present and future, is still a matter of debate. Some atmospheric inversion studies have suggested a large sink for anthropogenic CO₂ within the boreal forest region (Tans et al., 1990; Ciais et al., 1995; Kaminski et al., 1999; Ciais et al., 2000), though such

results are by no means ubiquitous (Rayner et al., 1999; Fan et al., 1998). Moreover, it has been argued on both observational (Schulze et al., 1999) and theoretical grounds (Lloyd, 1999) that boreal forests are unlikely to constitute a major sink for anthropogenic CO₂ at the current time.

Confounding such arguments are numerous observations that significant changes in the climate of boreal regions over the last 100 yr or so have already occurred. These changes, recently summarised for the high-latitude region of the northern hemisphere by

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Serreze et al. (2000), are well documented for the former USSR; they include changes in air temperatures (Groisman et al., 1994) duration and extent of snow cover (Groisman et al., 1994; Brown, 2000), precipitation intensity and amount (Groisman et al., 1999; Groisman and Rankova, 2001) and cloud-type frequency and amount (Sun and Groisman, 2000; Sun et al., 2001). It has also been argued that these changes in climate, particularly the well documented increase in temperatures over the last 20 yr or so, have already resulted in large-scale changes in the high northern latitude terrestrial CO₂ exchange (Randerson et al., 1999). Those authors argued that changes in the phasing of the seasonal cycle of CO₂ at high-latitude northern hemisphere sites were correlated with large-scale year-to-year variations in both spring and autumn temperatures. This suggests that long-term changes in the magnitudes of both photosynthesis and respiration may already be occurring in the high-latitude northern environment at the current time.

The net carbon balance of an ecosystem represents a subtle balance between photosynthesis and respiration (Grace et al., 1996), and it is not straightforward to predict whether such changes in climate and CO₂ exchange patterns should result in net loss or gain of carbon by the affected ecosystems. However, one common concern is that increases in temperature may result in significant losses of carbon from these ecosystems due to enhanced respiration rates (e.g. Ludeke et al., 1995). Indeed, long-term eddy covariance studies in both Canada and Sweden have found mature boreal forests to be significant sources of CO₂ to the atmosphere in warmer years (Goulden et al., 1998; Lindroth et al., 1998), this being attributed in both cases to enhanced rates of ecosystem respiration associated with the higher temperatures during these times.

Similar to these studies, we here report on the first long-term measurements of the carbon balance of a boreal forest in European Russia, presenting data from measurements undertaken between May 1998 to December 2000. We find, as was the case for observations in Scandinavia and Canada, that the forest studied here is a source of CO₂ to the atmosphere.

2. Materials and methods

2.1. Site description

The experimental site was located in the Central Forest Reserve (CFR) at Fyederovskoye, near the town of Nelidovo (Tver region), about 300 km WNW of

Moscow in European Russia (56° 27'N, 32° 55' E; ca. 220–270 m a.s.l.). The reserve was established in 1931, but in the 1950s and 1960s some exploitation for commercial logging was permitted. A detailed description of the physical geography different vegetation types within the reserve is given in Vygodskaya et al. (2002).

The eddy tower was mounted in a 150-yr-old forests spruce forest of *Sphagnum-Vaccinium myrtillus* type. This is a widespread forest type in northern, central and southern taiga, but is mostly limited to the middle and lower parts of soft slopes and shallow depressions with peaty podzolic gley soils, very weak surface runoff and high ground-water level. This forest type accounts for 7% of the total CFR forest area (Karpov and Schaposhnikov, 1983). These stands are typically characterised by simple vertical structure and long-lasting periods of flooding by temporary perched water, low oxygen content (0.1–3.2 mg L⁻¹) of ground water, poor soil aeration, low soil nitrogen content (0.5–9.9 kg ha⁻¹) and acidic reaction to the depth of >100 cm [pH(H₂O) in the range 3.53–3.83 in the 0–40 cm soil layer] (Karpov, 1973; 1983). The main stock of soil carbon is concentrated in peat horizon and has been estimated for the measurement site at 197 tC ha⁻¹ (Schulze et al., 2002). The soil root layer is 0–20 cm. The low shrub-grass layer is dominated by *Vaccinium myrtillus* and *V. vitis-idaea*, and the moss layer is typical with *Sphagnum girgensohnii* and *S. magellanicum*. Within the ground layer *Pleurozium schreberi*, *Hylocomium splensens* and *Polytrichum commune* occur as well (Abrajko, 1973). The stand is approximately 27 m high, consisting of about 86% *Picea abies* trees and about 14% *Betula* spp. with a total live tree density of 565 ha⁻¹ in 2000 (Vygodskaya et al., 2002). Above-ground woody biomass is approximately 63 tC ha⁻¹ (Schulze et al., 2002) with a projected leaf area index of about 3.5 (Schulze et al., 1999).

The measurement tower is situated in a shallow depression. The territory around the tower is rather heterogeneous. The dominant spruce stand is limited in extent, and within 200–300 m from the tower there are birch and aspen forests as well as windfall of different ages. A comprehensive footprint analysis of the area around the tower, taking into account the heterogeneous nature of the vegetation beyond the spruce stand, has been made by Sogachev et al. (2002). They suggested that typically around 80% of the measured flux originates from within a 200 m radius during the day, with the effective footprint being somewhat larger at night.

2.2. Instrumentation

Eddy covariance measurements of carbon dioxide, water vapour, heat and momentum fluxes were measured at a height of 31 m, about 4 m above the average tree height and 2 m above the highest nearby trees. The relatively low height of the measurement system was dictated by engineering constraints (no more tower parts), and it consisted of a triaxial sonic anemometer (model Solent R3, Gill Instruments, Lymington, UK) and a fast response CO₂/H₂O non-dispersive infrared gas analyser (IRGA) (model 6262-3, LiCor Inc., Lincoln, NB, USA). The air was drawn from an inlet at the top of the tower, 20 cm below the sonic measurement height through BEV-A-Line tubing (33 m length and 5 mm inner diameter) and two aerosol filters (ACRO 50 PTFE 1 µm pore-size, Gelman, Ann Arbor, MI, USA) at a flow rate of 4–5 L min⁻¹ (pump unit: KNF Neuberger, Germany). Output from the sonic anemometer and infrared gas analyser were read at 20 Hz through RS-232 ports onto 386-class computers, and all data stored for subsequent analysis. The pressure in the IRGA cell, as measured by the internal pressure sensor, was about 10 hPa above ambient.

Ambient CO₂ concentrations at heights of 0.2, 1.0, 2.0, 4.8, 10.8, 15.6, 25.2 and 28.0 m were recorded with a system consisting of a LiCor nondispersive infrared gas analyser (model 6251, LiCor Inc., Lincoln, NB, USA), pump (KNF, Neuberger, Germany), switching manifold, BEV-A-Line tubing and datalogger (Campbell, model CR23X). Air was drawn through the tubes at a rate of 7 L min⁻¹, with each height being sampled for 2 min, with readings taken at a rate of 1 Hz over the last 10 s of sampling at each height and averaged before being stored.

The measurement tower was also equipped with instruments to measure incoming photosynthetic photon flux density (model LI-190SA, LiCor Inc., Lincoln, NB, USA), humidity and temperature (model HMP35D, Vaisala, Helsinki, Finland), air pressure (model PTB101B, Vaisala, Helsinki, Finland), wind velocity (model A100R, Vector Instruments, Rhyl, UK), incoming and reflected solar radiation (model CM14) and net all-wave radiation [model LXG055 (Schulze-Däke), Dr. Bruno Lange GmbH, Berlin, Germany]. Precipitation was collected within the canopy on the height of 1 m above ground and was measured by a tipping bucket rain gauge (model 52202, R. M. Young Company, Traverse City, USA).

Five soil heat flux plates (model Rimco HFP-CN3, McVan Instruments, Melbourne, Australia) installed

at a depth of 4–5 cm were used to obtain an average soil heat flux in the neighbourhood of the tower. Soil temperature was measured by sensors PT 100 at two profiles at depths of 5, 15, 50 and 100 cm and then averaged for every depth. All meteorological data were collected every 10 s, and 10 min averages or sums (precipitation only) were stored on a datalogger (DI 3000, DeltaT, Burwell, UK).

2.3. Flux calculations and corrections

After linear detrending the fluxes were calculated offline using covariances of 30 min high-frequency time series of vertical wind velocity and temperature, CO₂ density and water vapour density. The time lag between measurements of vertical wind velocity and scalar densities due to transport in the tube was estimated by cross-correlation between both time series to be equal to approximately 7.0 s for carbon dioxide and 7.5 s for water vapour. The data were corrected by shifting the time series by the estimated time lag.

Frequency losses due to damping in the tube and analyser response were corrected using the approach of Eugster and Senn (1995). The correction parameter (“inductance”) was determined from the cospectral analysis of vertical wind, temperature, carbon dioxide and water vapour time series. For CO₂, the main subject of this paper, values were typically in the range 0.15–0.20. Water vapour dilution corrections were made with internal software of the LiCor 6262 and corrections of differences of the air pressure in the sampling cell and in the atmosphere were calculated automatically with the built-in pressure transducer. Coordinate rotation as in McMillen (1988) was applied.

At night under stable conditions when the vertical transport is suppressed, large amounts of CO₂ can accumulate between soil surface and the measuring height. To account for the flux that is associated with the change in storage of CO₂ in the air column between measuring height and surface, this storage term was calculated as the change of the density of carbon dioxide molecules per unit ground area over time and summed with the measured eddy covariance flux to provide and estimate of the net ecosystem exchange (N_E).

The data quality was checked using a stationarity test (Foken and Wichura, 1996). Non-stationary data (the sum of the variances of six 5-min intervals of a time series deviated more than 50% of the variance of the total 30-min interval) were excluded from further

analysis, except for calculating cumulative fluxes of carbon dioxide and water vapour in cases where data points still seemed to be realistic. Small gaps (up to 2 h) due to instrumental errors or after rejection were filled using interpolation; larger gaps were filled with empirical regressions for respiration and assimilation (see below). In total, usable data were available for 85% of the time during the 27 months of measurements.

3. Results and discussion

3.1. Climatology

Seasonal trends in daily average air and soil temperatures are shown in Fig. 1 for the study period. In general, air temperatures increased from March until June, remaining relatively warm up until late September, after which a rapid decline occurred: air temperatures typically being below 0 °C between November and March. However, thaws of 2–5 d duration with an average daily temperature of 2–4 °C also occurred in both winters. Spring frosts at nights caused by an intrusion of cold arctic air masses also occurred on several occasions in April and May during both 1999 and 2000.

The seasonal amplitudes of soil temperatures at all depths were significantly less than those of air temperature and of lower magnitude, and with less high fre-

quency variations at depth. The date of maximum soil temperatures occurred significantly later than that for air temperatures, with the maximum lag of 2 months being observed at 100 cm depth (9 °C in mid-August). Soil temperatures at 5 cm depth fell below zero only in the winter of 1998/1999 and were never less than –0.6 °C. The soil temperature at all deeper depths in other winter seasons remained above 0 °C in both years. This was despite average daily air temperatures as low as –23 °C (Fig. 1). Maximum air temperatures and soil temperatures at all depths during summer tended to be higher in 1999 than was the case for either 1998 or 2000. The relatively high and constant soil temperatures probably represents the “zero curtian effect” where, in the presence of an insulating snow cover, the release of latent heat upon the fusion of H₂O results in temperatures being maintained near 0 °C for a considerable length of time in a refreezing or thawing active layer (Sumgen et al., 1940; Outcalt et al., 1990).

Using data from the weather station of Vyshnij Volochok, which is located about 160 km from the measurement site (57.35°N, 34.34°E; ca.161 m a.s.l.), mean monthly temperatures and total monthly precipitation for the measurement period are compared with long-term averages (1891–1988) in Table 1. This shows the summer of 1998 to be considerably moister and colder than the long-term average. However, the opposite pattern was observed in 1999, with air temperatures in June and July 1999 being 3–5 °C higher

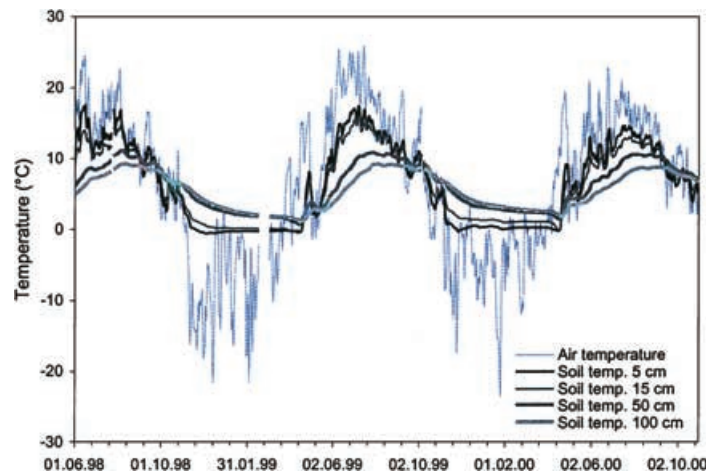


Fig. 1. Observed daily average air (blue line) and soil temperature (red line, at 5 cm depth; green line, 100 cm depth) from June 1998 to November 2000. In contrast to air temperature, soil temperature at 100 cm is of much less amplitude and in winter hardly reached –0.5 °C.

Table 1. Comparison of average monthly air temperature T and precipitation P for the study period and the long-term climatic average (1891–1988)^a

	January	February	March	April	May	June	July	August	September	October	November	December
T ₁₉₉₈ , °C						17.4	16.3	13.7	10.3	4.5	-9.0	-7.3
T ₁₉₉₉ , °C	-6.0	-9.7	-0.8	9.2	7.9	20.9	20.3	15.0	11.5	5.0	-3.7	-2.9
T ₂₀₀₀ , °C	-7.2	-3.5	-1.7	9.4	10.1	14.2	16.8	15.2	10.7			
T _{avg} , °C	-9.8	-9.1	-4.2	3.6	11.1	15.2	17.2	15.5	10.1	4.1	-1.9	-7.0
P ₁₉₉₈ , mm						62.7	190.2	135.3	80.7	40.7	14.0	14.6
P ₁₉₉₉ , mm		33.6	8.6	20.5	37.0	91.6	108.2	129.4	68.9	97.5	23.8	85.6
P ₂₀₀₀ , mm	14.7			54.2	11.8	86.4	86.3	14.6	7.9	23.5	11.8	
P _{avg} , mm	30.6	28.4	28.7	31.9	50.7	73.4	87.0	71.0	58.2	46.5	40.5	37.4

^a All data come from the meteorological station Vyshnij Volochook, located about 160 km from the study site.

than normal. The beginning of summer 1999 was one of the five hottest on record. The unusually warm April temperatures occurred both in 1999 and 2000, resulting in the highest monthly averages on record except April 1921.

The monthly precipitation for May–December 1998 was 538.2 mm, and for 1999 was 646.2 mm, which is 30% and 11% higher than climate averages. The greatest variations of precipitation occurred in July and August 1998, for which the precipitation amount was about 100% greater than the long-term average.

Daily precipitation sums for Fyederovskoye are also shown in Fig. 2, along with daily photosynthetically active radiation (PAR) integral values. As with Table 1, this shows that much of the precipitation occurs during the growing season (70% from early April until early October). The unusually wet period in July 1998 is also illustrated well here, with most intensive rain day occurring on 29 July 1998 with over 65 mm falling. This extreme event resulted in the water table being above the soil surface for more than one week.

As is discussed by Schulze et al. (2002), climatologically the study region is located in a transition between a West European oceanic climate and a continental climate with North Atlantic air masses altering in a 3–7 d cycle with cold polar air masses. Associated with the rapid changes in air mass than can occur are frequent heavy storms, such as can be seen from the high daily precipitation totals that sometimes occur during summer (Fig. 2). Schulze et al. (2002) and Vygodskaya et al. (2002) have argued that,

along with the extended dry periods that can occur in some years, the frequency of such heavy storms may exert an important influence on forest carbon balances by virtue of enhanced tree mortality, especially by extreme windthrow events. Groisman et al. (1999) have shown that the frequency of high precipitation (storm) events, characterised by a daily precipitation greater than 20 mm, has actually increased in European Russia by 19% over the last 50 yr.

The seasonal trends of PAR show the expected strong dependence of PAR on time of year in northern boreal climates, with the maximum daily PAR integrals increasing from $5 \text{ mol m}^{-2} \text{ d}^{-1}$ in winter to $25\text{--}30 \text{ mol m}^{-2} \text{ d}^{-1}$ near both spring and autumn equinox and then increasing further up to $56\text{--}58 \text{ mol m}^{-2} \text{ d}^{-1}$ near the summer solstice (Fig. 2). There were, however, considerable day-to-day variations in PAR integrals during the study period, especially during the summer period as a consequence of considerable day-to-day variations in cloudiness. These have an effect of the same magnitude as the seasonal variations. Variations from one day to another were as much as $25\text{--}30 \text{ mol m}^{-2} \text{ d}^{-1}$ in summer, with an average difference of $10\text{--}12 \text{ mol m}^{-2} \text{ d}^{-1}$ (Fig. 2).

3.2. The relationships between night-time respiration rates and soil and air temperatures

In order to obtain a reliable estimate of the carbon balance of an ecosystem using the eddy covariance technique, it is necessary to ensure that no systematic

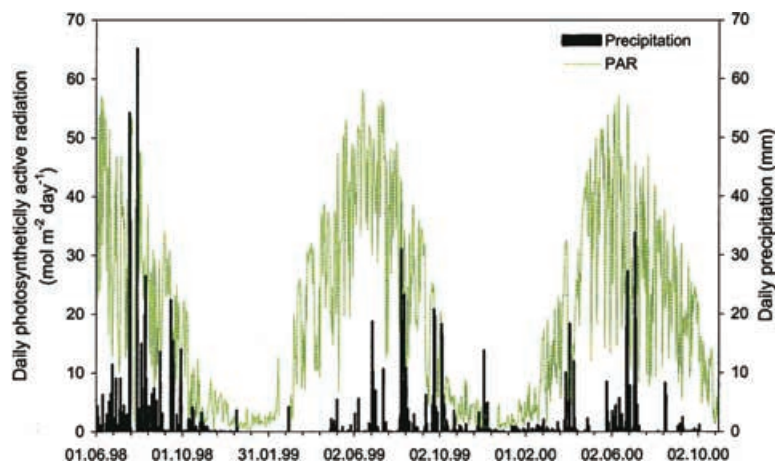


Fig. 2. Observed daily total PAR (solid line) and daily precipitation (vertical bars) from June 1998 to November 2000. Very strong rain events frequently occurred during the 1998 growing season.

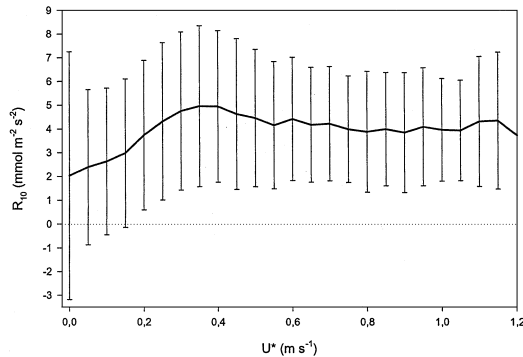


Fig. 3. The relationship between night-time ecosystem respiration rate adjusted to a value of 10 °C (R_{10}) and friction velocity (u_*). Data have been binned into u_* classes of 0.05 m s⁻¹ and means of standard errors of 30 min estimates are shown.

biases in the measurements occur (Moncrieff et al., 1996). In this context, it is of concern that quite often ecosystem CO₂ efflux rates seem to be reduced under conditions of low turbulence, especially under stable atmospheric conditions at night (Goulden et al., 1996; Jarvis et al., 1997; Lindroth et al., 1998; Markkanen et al., 2001). To qualify the possible importance of this effect we investigated the relationship between the measured night-time fluxes and friction velocity u_* . This showed, as has also been observed in some other studies, that the inferred night-time ecosystem respiration rates were much reduced below about $u_* = 0.35$ m s⁻¹ (Fig. 3). As the above calculation included an estimate of any changes in the “storage” within the canopy, this “loss of flux” is presumably due to an inability of the eddy covariance technique to measure fluxes adequately under stable atmospheric conditions with strongly suppressed turbulence or problems due to flux divergence or intermittent turbulence (Goulden et al., 1996)

It is thus desirable to substitute for these apparently underestimated fluxes at low u_* in order to obtain an accurate estimate of the ecosystem C balance (Goulden et al., 1996). As ecosystem CO₂ effluxes should reflect soil (including roots) as well as stem and foliage, respiration dependencies on both soil and air temperatures should be apparent. From Fig. 1 it is clear that, especially in the presence of snow cover, the relationship between air and soil temperatures is not straightforward, when quite stable soil temperatures are associated with large variations of air temperature.

To describe joint effects of both air and soil temperature we introduce the coefficient a that allows for

a joint effect of both soil temperature and air temperature on the ecosystem respiration rate, fitting an Arrhenius-type function:

$$R_{\text{canopy}} = R_{10} [a \exp S/R (1/T_{\text{soil}} - 1/283.15) + (1 - a) \exp A/R (1/T_{\text{air}} - 1/283.15)] \quad (1)$$

where R is the universal gas constant (8.314 J mol⁻¹ K⁻¹), T_{soil} and T_{air} are air and soil temperature in K, R_{10} is the respiration rate at 10 °C (6.28 μmol m⁻² s⁻¹ in our case) and S and A are fitted parameters equivalent to an Arrhenius-type activation energies (equal to 112 131 J mol⁻¹ and 80 405 J mol⁻¹, respectively).

According to our model fit, $a = 0.83$. This means that when soil and air temperatures are both at 10 °C, 83% of night-time respiration would be accounted for soil temperature (soil respiration) and 17% for air temperature. The relationship between measured and modelled values is shown in Fig. 4. This shows the model to provide an excellent fit to the data at lower rates, but that the ability of the model to account for variability in respiration rates is lower at higher values. Nevertheless, even for the higher measured respiration rates the model is an unbiased predictor of ecosystem respiration, and there is no systematic bias of the model with respect to air or soil temperatures or with the time of year (data not shown). One possibility to account for the large fluctuations in respiration rates at higher temperatures may be that variables other than temperature are involved, for example possible large releases of carbon dioxide from previously anoxic soil

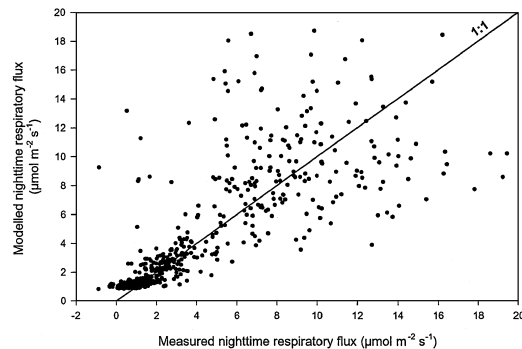


Fig. 4. Modelled vs. observed respiration fluxes using the combined air and soil temperature model. Each point is the average flux over one night. Night was defined as period when PAR is less than 10 mmol m⁻² s⁻¹. Respiration fluxes were calculated by eq. (1).

associated with seasonal decreases in water table depth during drier periods.

3.3. Estimation of annual values for Gross Primary Production (GPP), ecosystem respiration and the canopy carbon balance

The CO₂ flux between spruce forest and the atmosphere, usually termed the net ecosystem exchange (N_E), is the difference of ecosystem respiration (R_E) and the gross primary productivity of the photosynthesising vegetation (GPP)

$$N_E = R_E - GPP, \quad (2)$$

where here any mitochondrial respiration by the leaves during the day is considered as a debit on the net CO₂ assimilation rate, which for our definition here is equivalent to GPP [see also Shibistova et al. (2002) and Lloyd et al. (2002) for a more detailed discussion of this issue]. In order to partition the observed daytime N_E into GPP and R_E we must first consider that respiratory processes are connected with needles (dark-respiration), tree stems and roots and microbial activity. It seems reasonable to assume that daytime microbial and root respiration should show no intrinsic dependence upon time of day and a strong correlation with soil temperature. Likewise, daytime stem and branch respiration should be related to air temperatures with much the same relationship as is observed in the dark. The rate of “dark” respiration by needles during the day is, however, unknown. However, based on laboratory observations, it is almost certainly substantially less than that that would occur at the same temperature at night (Brooks and Farquhar, 1985; Villar et al., 1995). We circumvent this problem for daytime estimates of R assuming that 20% of the night-time respiration considered to be dependent on air temperature is attributable to stem respiration, with the remaining 80% being accounted for by the needles. This estimate is based on a ratio of night-time foliage respiration to stem respiration rates as has been observed in other studies. For example, examining a range of Canadian boreal forests, Ryan et al. (1997) estimated ratios between 2:1 and 5:1 (depending on the forest), and Shibistova et al. (2002) inferred a ratio of about 4:1 for a Siberian pine forest. Thus, during daylight hours, the non-soil respiratory component is taken here as only 0.2 of that suggested by eq. (1).

Daytime fluxes for small (<2 h) missing data periods were also interpolated. Larger data gaps were filled by using empirical coefficients (a_{\max} , b , c) of the sim-

ple PAR regression determined from 5 previous and next days with available data:

$$N_E = A_{\max} \text{PAR} / (b + \text{PAR}) + c,$$

where A_{\max} represents the maximum (light-saturated) photosynthetic rate, and b and c are constants that describe the shape of the light response curve and the magnitude of the ecosystem respiratory flux, respectively.

Daily GPP and R_E partitioned using the above assumptions, as well as the accumulated CO₂ flux, are presented in Fig. 5. Here simulations have been done for two assumptions regarding the possible loss of night-time flux at low friction velocities. In one simulation all night-time measurements made for $u_* < 0.35 \text{ m s}^{-1}$ have been rejected, and estimates for the actual flux during these periods made according to eq. (1). In the second case, all measured night-time respiratory fluxes have been accepted. In both cases respiratory fluxes for small (<2 h) missing data periods were interpolated and for bigger missing periods they were calculated using eq. (1). It should be noted that the storage calculations have been included for both daytime and night-time measurements, and we do not believe that there has been any double counting induced for the case of the model being used as a substitute for measurements under conditions of low night-time turbulence. That is, of course, unless there are systematic errors in the storage calculation itself. However, we certainly cannot think of any straightforward reason why that would be the case.

Figure 5 shows that even for the case where all night-time measurements are accepted, R_E exceeds GPP at this site for almost all of the year, the only exception being beginning of growing season (from early April until June). When data for which $u_* < 0.35 \text{ m s}^{-1}$ are excluded and substituted for using eq. (1), it emerges that there is hardly any time of the year for which this forest is a net sink of CO₂. This is because substitution of data for which $u_* < 0.35 \text{ m s}^{-1}$ with estimates from eq. (1) increases the estimated R_E by about 18–20% for both 1999 and 2000, with the effect being somewhat smaller for the period June–December 1998 (Table 2). Thus, as was also shown by Grelle (1997) and Lindroth et al. (1998), correction of night-time respiration fluxes for a loss of flux at low u_* drastically increases the inferred carbon balance. For the “uncorrected” night-time fluxes N_E is 3–6 mol CO₂ m⁻² yr⁻¹, whereas for the “corrected fluxes” N_E is much greater, 26–27 mol CO₂ m⁻² yr⁻¹. However, irrespective

Table 2. Values of annual gross primary production and ecosystem respiration estimated with and without correction of fluxes measured at low u_*

Period	Gross photosynthesis, mol m ⁻² period ⁻¹	Respiration (corrected values at $u_* < 0.35$ m s ⁻¹), mol m ⁻² period ⁻¹	Respiration (non-corrected values below $u_* < 0.35$ m s ⁻¹), mol m ⁻² period ⁻¹
June–December 1998	93	108	93
January–December 1999	122	149	125
January–December 2000	102	128	108

^aFor both cases respiration exceeds gross photosynthesis by 16–25%.

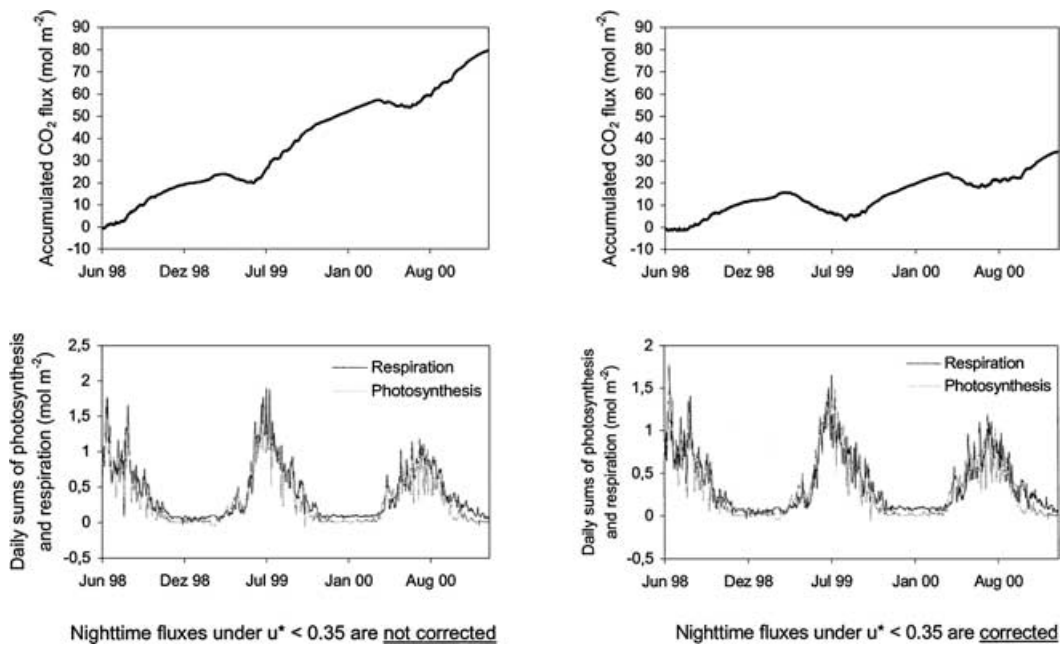


Fig. 5. Accumulated CO₂ flux and daily course of gross photosynthesis and respiration calculated for the whole period of measurements (June 1998 to December 2000). (a) Models of daytime dependence of PAR and of night-time dependence of soil and air temperature are used only for filling gaps. (b) The same models are used for both gaps filling and for replacement of CO₂ flux values measured during windless nights ($u_* < 0.35$ m s⁻¹). Night-time measurements for $u_* < 0.35$ m s⁻¹ have been simulated according to eq. (1).

of whether or not adjustments for possible night-time flux losses are applied, this forest is inferred to currently be a significant source of CO₂ to the atmosphere (Fig. 5, Table 2).

The gross primary production of the site (*GPP*) is estimated to be 102–122 mol CO₂ m⁻² yr⁻¹ (Table 2). This value is similar to values cited for two Swedish boreal forests, around 100 mol C m⁻² yr⁻¹ for two stands in Sweden and slightly higher than the

85 mol C m⁻² yr⁻¹ calculated for a 30-yr-old regenerating stand in southern Finland. (Lindroth et al., 1998; Valentini et al., 2000; Markkanen et al., 2001). However, the *GPP* of the forest studied here is over twice the value of 45 mol C m⁻² yr⁻¹ estimated for a Scots pine forest in central Siberia using a similar methodology (Shibistova et al., 2002). This may be explained on the basis of the significantly shorter growing season for the Siberia site (about 90 d versus 130 d here:

threshold temperature = 10 °C; Schulze et al., 2002) as well as the large differences in LAI (1.5 in Siberia and about 3.5 for the forest studied here). Compared to the coniferous forests of Canada, our *GPP* estimate is about 2-fold higher. For four relatively mature forests studied as part of the BOREAS study, Ryan et al. (1997) obtained $GPP = 60 \pm 10 \text{ mol C m}^{-2} \text{ yr}^{-1}$.

3.4. Possible explanations for the negative carbon balance

Most forests whose annual carbon balance has been estimated to date using the eddy covariance technique appear to be net carbon sinks (Grace et al., 1995; Goulden et al., 1996; Malhi et al., 1999; Valentini et al., 2000; Jarvis et al., 2001), the only major exceptions being the Swedish boreal forest studied by Lindroth et al. (1998) and the Canadian boreal forest studied by Goulden et al. (1998). Like these other two boreal forests, the European Russian boreal forest studied here is also a significant source of CO₂ to the atmosphere and of an even greater magnitude than the Swedish or Canadian studies. For the Swedish forest and using a methodology for the correction of night-time fluxes similar to that used here, Lindroth et al. (1998) estimated their forest to be a net source of 21 mol C m⁻² yr⁻¹ for 1995 and 7 mol C m⁻² yr⁻¹ for 1996; Janssens et al. (2001) noticed that significant soil disturbance occurred at that site, and Grelle (personal communication) has suggested that changes in the height of the water table in previous years may also be involved. Goulden et al. (1998) found their Canadian boreal forest of lower productivity to be a more modest source, on average about 2.5 mol C m⁻² yr⁻¹ between 1994 and 1997. For the forest studied here, the corrected data suggest a source of about 30 mol C m⁻² yr⁻¹ for both 1999 and 2000, suggesting that respiration exceeded photosynthesis by more than 25% in both years.

Two possible explanations for this significant imbalance between R_E and *GPP* readily come to mind. One is that the imbalance has arisen because of enhanced R_E and/or reduced *GPP* in the study period due to some unique features in the short or long-term disturbance history of the site (e.g. Amiro, 2001; Janssens et al., 2001; Knohl et al., 2002; Wirth et al., 2002) or simply as a consequence of the almost universal changes in productivity that occur with stand age (Ryan et al., 1997; Lloyd, 1999; Smith and Long, 2001;

Wirth et al., 2001). Second, it could be that short- or long-term changes in climate have resulted in the current carbon imbalance in the measurement stand (e.g. Goulden et al., 1998; Lindroth et al., 1998; Vaganov et al., 1999).

3.4.1. Site history. One possibility to account for the negative carbon balance is that the rate of respiratory release from the study forest is currently high due to high rates of decomposition of coarse woody debris (CWD). The strong droughts of 1992 caused the thin surface roots to die off and for many trees to fall under the influence of strong winds in a storm in 1996. As a result a volume of fallen trees on the ground at the current time is much greater than in the past (Vygodskaya et al., 2002). Nevertheless, a simple order-of-magnitude calculation suggests that any increased respiratory flux from this higher than usual amount of CWD is unlikely to be sufficient to account for the substantial carbon source observed. For example, the carbon density of the fallen trees is currently about 160 mol C m⁻². (Vygodskaya et al., 2002). Taking a mean residence time for carbon in decomposing wood of 0.05 yr⁻¹ as determined in a nearby windthrow area (Knohl et al., 2002), this then equated to a rate of carbon loss from the decomposing wood of only about 8 mol C m⁻² yr⁻¹. Of this, only about 50% would be respired rather than entering the soil carbon pool (Harmon et al., 1986), which suggests that the increased ecosystem respiratory flux as a consequence of higher than usual tree mortality in 1996 should be about 4 mol C m⁻² yr⁻¹. Whilst appreciable, this is substantially less than the magnitude of the net respiratory source for this forest of about 20–30 mol C m⁻² yr⁻¹, which suggests that, if we accept the need to correct for a loss of fluxes at low friction velocity (Table 2) then some other factor must be involved.

3.4.2. Dependence of net ecosystem productivity on climate. Both Lindroth et al. (1998) and Goulden et al. (1998) suggested that higher temperatures over the last decade or so may be responsible for their forests currently being carbon net sinks. There is also some supportive evidence for this from other flux studies in boreal forests. For example, working in a black spruce stand in Canada, Jarvis et al. (1997) observed that on hot sunny days their forest seemed to be a source of CO₂, whereas on cooler and even cloudy days the forest was a net sink. A second possibility is the changes in incoming PAR as a consequence of the well documented variations in cloudiness that

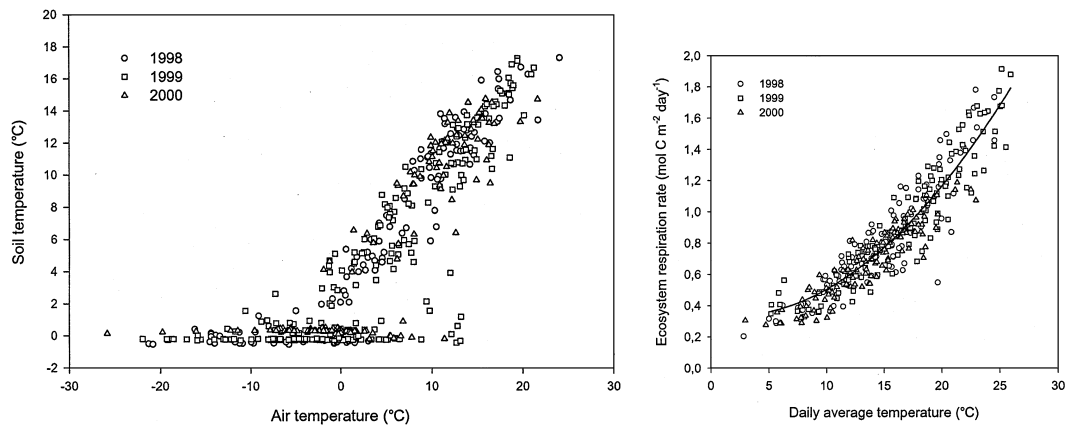


Fig. 6. The relationship between estimated daily ecosystem respiration rate and daily mean air temperature for the years for the periods from 1 June to 30 September. Daily ecosystem respiration rate has been calculated by a procedure described in Section 3.3. Different symbols represent different calendar years.

have occurred over the former Soviet Union over the last century and especially since the 1950s (Sun and Groisman, 2000; Sun et al., 2001). In attempt to quantify the relative magnitude of these effects we examined the relationship between daily average soil temperatures and daily ecosystem respiration rate, estimated as described in Section 3.2 with daytime estimates of RE coming from eq. (1) (but with no foliar respiration) and with eq. (1) being used to substitute for night-time measurements only when $u^* < 0.35 \text{ m s}^{-1}$. We have used daily mean air temperature, taking data for all years from 1 June to 30 September (Fig. 6). This shows that there was a reasonably strong (albeit not perfect) relationship between air and soil temperatures during this time (Fig. 6a), suggesting that for this period of the year, daily average air temperature should be reasonable empirical predictor ecosystem respiration rate. Indeed, as is shown in Fig. 6b, a strong non-linear relationship between ecosystem respiration rate and daily average air temperature was observed.

We then examined the relationship between daily *GPP* as inferred from the flux measurements and our ecosystem respiration measurements and daily PAR integral. This is shown in Fig. 7. This shows the expected positive relationship between *GPP* and PAR, but with substantial scatter. Nevertheless, there are some indications of a plateau above about $35 \text{ mol quanta m}^{-2} \text{ d}^{-1}$. In order to see if any of this variation was accountable for by variations in temperature we therefore examined the relationship between daily *GPP* and average daily temperature for all days

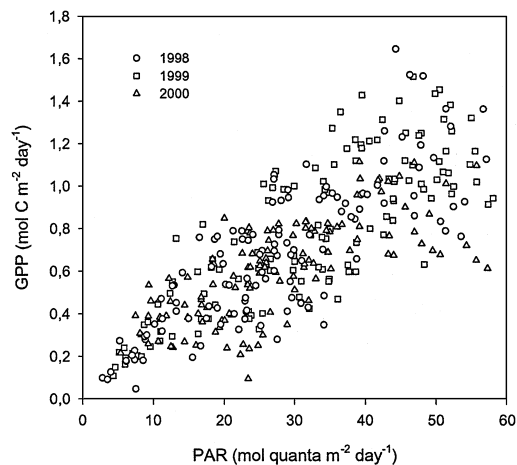


Fig. 7. The relationship between daily *GPP* and daily PAR integral. Daily *GPP* is calculated as a sum of half-hourly values inferred from the eddy flux measurements and ecosystem respiration simulated as described in Section 3.3. The expected positive relationship between *GPP* and PAR is compounded by substantial scatter. Different symbols represent different calendar years.

with a PAR integral greater than $35 \text{ mol quanta m}^{-2}$. This is shown in Fig. 8, which clearly indicates that at high PAR, *GPP* increases with temperature for this forest, with no obvious temperature optimum being reached. This suggests that the *GPP* of this forest is always to some extent limited by temperature under

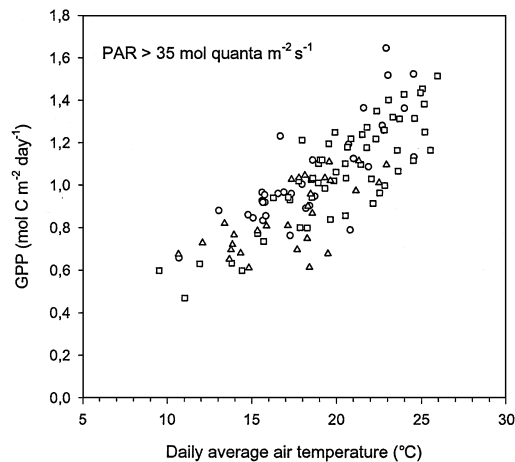


Fig. 8. The relationship between daily *GPP* and average daily temperature for sunny days (with a PAR integral greater than $35 \text{ mol quanta m}^{-2} \text{ s}^{-1}$). There is no obvious temperature optimum for photosynthesis. Different symbols represent different calendar years.

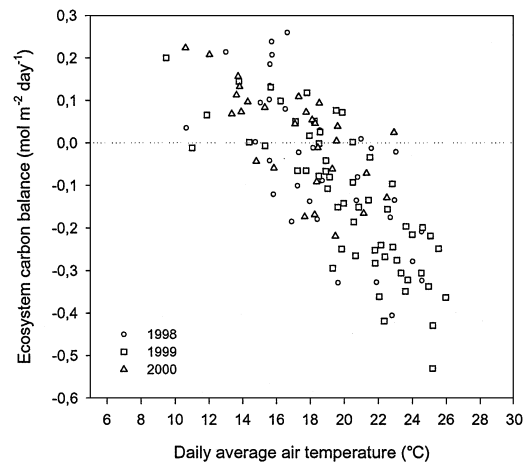


Fig. 9. The relationship between daily ecosystem carbon balance and average daily temperature for days with a PAR integral greater than $35 \text{ mol quanta m}^{-2} \text{ s}^{-1}$. On sunny days ecosystem carbon balance seems very sensitive to ambient temperatures. Different symbols represent different calendar years.

current day climatic conditions. However, most importantly on sunny days the rate of carbon loss from this ecosystem is more sensitive to temperature than is the rate of carbon gain via photosynthesis. This can be seen from an examination of the dependence of NEP on temperature, also only using data from days with a daily PAR integral of more than $35 \text{ mol quanta m}^{-2}$ (Fig. 9). Clearly then, as has been observed for other forests (Jarvis et al., 1997; Lindroth et al. 1998), the boreal forest here seems to loose carbon under conditions of elevated temperatures.

4. Conclusions

Over the period examined the study forest was a substantial source of CO_2 to the atmosphere. As has also been pointed out by Grelle (1997) the magnitude of the source is dependent on whether corrections are made for the apparent loss of flux under low turbulence conditions, such as typically occur at night. If these corrections are not made, then the forest is only a modest source of $3\text{--}5 \text{ mol C m}^{-2} \text{ yr}^{-1}$, and this may be accountable for by higher than usual rates of tree mortality for the decade prior to the flux measurements. However, if the need for such corrections is accepted, then the forest is a calculated to currently

be a substantial source to the atmosphere: somewhere between 20 and $30 \text{ mol C m}^{-2} \text{ yr}^{-1}$. This suggests that some factor other than site history must be involved. Examination of the daily carbon balance and the component photosynthetic and respiratory fluxes suggests that the forest should be a larger source of carbon to the atmosphere in warmer years. Although both photosynthesis and respiration increase markedly with increasing temperatures, for this ecosystem the temperature sensitivity of respiration is clearly greater than is the case for photosynthetic carbon acquisition.

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