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ABSTRACT

Net ecosystem–atmosphere exchange of CO_2 (NEE) was measured in two boreal bogs during the snow-free periods of 1998, 1999 and 2000. The two sites were located in European Russia (Fyodorovskoye), and in central Siberia (Zotino). Climate at both sites was generally continental but with more extreme summer–winter gradients in temperature at the more eastern site Zotino. The snow-free period in Fyodorovskoye exceeded the snow-free period at Zotino by several weeks. Marked seasonal and interannual differences in NEE were observed at both locations, with contrasting rates and patterns. Amongst the most important contrasts were: (1) Ecosystem respiration at a reference soil temperature was higher at Fyodorovskoye than at Zotino. (2) The diurnal amplitude of summer NEE was larger at Fyodorovskoye than at Zotino. (3) There was a modest tendency for maximum 24 h NEE during average rainfall years to be more negative at Zotino (-0.17 versus -0.15 mol m^{-2} d^{-1}), suggesting a higher productivity during the summer months. (4) Cumulative net uptake of CO_2 during the snow-free period was strongly related to climatic differences between years. In Zotino the interannual variability in climate, and also in the CO_2 balance during the snow-free period, was small. However, at Fyodorovskoye the bog was a significant carbon sink in one season and a substantial source for CO_2-C in the next, which was below-average dry. Total snow-free uptake and annual estimates of net CO_2-C uptake are discussed, including associated uncertainties.

1. Introduction

Summarising data from boreal and subarctic sites Gorham (Gorham, 1991) estimated a carbon pool of 455 Pg, or one third of global soil carbon to be stored in northern wetlands. Other authors have derived smaller pool sizes (e.g. Sjörs, 1980) which draw

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attention to the large uncertainties behind estimates of C storage; these are largely associated with the peat depth and C density that is assumed in the analyses. Nonetheless there is no doubt that northern wetlands are amongst the world's most important long-term carbon reservoirs (Post et al., 1982; Botch and Massing, 1983; Zoltai and Pollett, 1983; Joiner et al., 1999). For an area of 68.5×10^{10} ha of Russian bogs, Turunen et al. (2001) estimate a storage of ca. 12×10^{12} g C ha^{-1} a^{-1}. In the absence of disturbances, northern wetland net carbon uptake rates are small and the observed C accumulation represents the fine

imbalance that exists between low productivity and even lower decomposition rates. Production rates are constraint by the often short growing seasons and relatively low nutrient availability and pH, while decomposition is suppressed in the anoxic and cool subsurface conditions (Gorham, 1991; Frolking et al., 1998; Brake et al., 1999; Christensen et al., 1999; Thormann et al., 1999). An additional factor contributing to the wetlands function as long-term C sinks is a relatively low frequency of fires (Turunen et al., 2001). In large parts of the forested areas of the boreal and subarctic biomes these regularly remove substantial amounts of carbon stored in forest biomass as well as in soils (Rapalee et al., 1998; Wirth et al., 1999).

It is because of this small difference between CO$_2$-C uptake during photosynthesis and its release during decomposition that the sink capacity in northern wetlands is considered to be vulnerable to changes in precipitation patterns and/or temperatures. A changed climatic regime may shift new peatland formation north, a consequence of possible melting of some permafrost areas exposed to higher temperatures, but in currently existing peatlands, warmer and drier conditions are envisaged to increase decomposition rates.

Long-term C accumulation in peatlands has been estimated from ^{14}C dating (Korhola et al., 1995; Trumbore et al., 1999; Turunen et al., 2001), but studies on the climatic regulation of seasonal and interannual variation of northern wetland CO$_2$ fluxes are scarce. Micrometeorological measurements provide information about the area-integrated, net ecosystem exchange of CO$_2$. These measurements can put valuable constraints on the long-term carbon storage estimates and scenarios of wetland response to climate change that are based on carbon dating or modelling exercises, although often the observations have to be limited to the spring–autumn period. In the remote boreal and subarctic environment, continuous data collection during winter is more or less impossible as temperatures can fall well below the technical limit of the instrumentation, and also the power supply cannot always be guaranteed. Nevertheless, from a few dedicated groups some information has become available for CO$_2$ exchange in boreal, subarctic and arctic wetlands (Neumann and den Hartog, 1994; Lafleur et al., 1997; Suyker et al., 1997; Aurela et al., 1998; Soegaard and Nordstroem, 1999; Valentini et al., 2000; Nordstroem, 2001). However, to date the data cover only in a limited number of cases more than one entire season (Shurpali et al., 1995; Griffis et al., 2000) and are with one excep-

tion restricted to measurements in fens (Lafleur et al., 2001).

In the following we report on three seasons of eddy covariance measurements of net ecosystem–atmosphere exchange (NEE) in two ombrotrophic bogs, one located in European Russia and the other in central Siberia. Objectives of the study were to analyse the seasonality and interannual variation in NEE based on climatic differences that existed between the two sites and between years. The measurements were conducted largely in the three snowfree periods between 1998 and 2000, but some data under snow were also collected. The study sites were located ca. 300 km NNW of Moscow and 30 km W of the Yenisey river, respectively. The latter site represents the world's largest peat basin, which is found between the Ob and Yenisey rivers (Walter, 1977; Gorham, 1991) in Siberia. The site near Moscow shows typical characteristics of the east European pine bog province (Botch and Masing, 1983).

2. Site description and methods

Measurements of ecosystem CO$_2$ and H$_2$O fluxes and associated climatic variables were conducted over three growing seasons at two bogs, one located in European Russia (named Fyodorovskoye, 56°27′N, 32°55′E), the other one in central Siberia (named Zotino, 60°45′N, 89°23′E). A detailed description of the sites is given in Kurbatova et al. (2002). Based on their vegetation and hydrology both wetlands were considered typical representatives of ombrotrophic bogs, but they differ somewhat in their microtopography. The Zotino site is characterised by a network of 40–60 cm tall *Sphagnum fuscum* ridges which were located above the water surface during the entire summer, separating hollows that are typically inundated for at least part of the season. The ridges cover approximately 40% of the bog's surface and are arranged in streaks, probably as a result of lateral meltwater flow and surface runoff from the surrounding forest growing on undulating sandy slopes. A range of vascular plants grows atop of the ridges, mainly *Chamaedaphne calyculata, Andromeda polifolia, Eriophorum vaginatum* and *Ledum palustre* which represent 40, 17, 16 and 15% of the aboveground biomass, respectively. Noticeable are also few scrawny (<1.5 m) *Pinus sylvestris* trees. The peat lawns in the hollows are formed largely by *Sphagnum cuspidatum*, vascular plant biomass is only ca. one third that of the ridges,

dominated by *Scheuchzeria palustris* and some *Carex limosa* (30 and 10%, respectively, of vascular above ground biomass in the hollows) (N. Savushkina, personal communication).

At Fyodorovskoye, the surface of the bog is much more flat and regular, and with no trees growing in the near vicinity of the eddy covariance tower. The area of free water during the growing season was also smaller there. Dominant species are *Eriophorum vaccinatum, Andromeda polifolia* and *Sphagnum rubellum*, with interspersed *Vaccinium oxyicoccus, Drosera rotundifolia* and - *anglica* and *Trichophorum cespitosum* (E.-D. Schulze, personal communication). We do not have any more detailed data on species cover or biomass for that ecosystem.

Being more continental, annual temperature and precipitation is much lower at the Zotino site compared to Fyodorovskoye. The average long-term temperatures measured at the township of Bor, located ca. 100 km to the north of the Zotino site is -1.5 °C and the average annual precipitation is 593 mm. About half of the annual precipitation falls as snow during winter (Arneth et al., 2002). Average annual precipitation at Fyodorovskoye exceeds precipitation in central Siberia (711 mm) but here, too, about 50% of the precipitation falls as snow. Despite the cold mean annual temperatures in Siberia, growing season temperatures (e.g. when average daily temperatures exceed 5 °C) are 13.4 °C.

In June 1998, in each of the two bogs a tower was instrumented with eddy covariance systems and sensors to measure environmental variables. The systems, data collection and corrections employed have been described before (Kurbatova et al., 2002) and closely resembled set-ups that were used during the Euroflux measurements (Aubinet et al., 2000). Identical systems were also employed in boreal forest ecosystems adjacent to the bog sites (Milyukova et al., 2002; Tchebakova et al., 2002).

3. Results and discussion

Measurements were conducted at Zotino in the periods 11/6/98–5/10/98, 10/4/99–15/11/99 and 1/4/00–18/10/00 (Figs. 1A–C). These overlapped with measurements at Fyodorovskoye which were undertaken during 14/6/98–12/10/98, 27/3/99–19/11/99 and 11/4/00–05/11/00 (Figs. 1D–F). Climate at both sites varied considerably from year-to-year (Table 1). For example, at Zotino, the year 2000 was relatively cool

and wet compared to the two preceding years. At Fyodorovskoye, the year 1999 was particularly dry and warm compared to the long-term average. At both sites, measurements covered the snowfree period but some data were also collected before snowmelt and after snowfall in autumn (Kurbatova et al., 2002). Despite the remoteness of the sites, data were collected continuously during the above periods, with the exception for several usually short interruptions (of less than 10 days duration as a consequence of instrument or power-supply failures). Unfortunately, due to problems with data collection at Fyodorovskoye during summer 2000 nearly two months of data were lost.

Instantaneous night-time fluxes

Careful quality control should be part of every analysis of eddy CO_2 fluxes. This is especially essential during periods of high atmospheric stability, such as they often develop during calm nights when turbulent transport is suppressed. In such circumstances it may not be possible to measure fluxes reliably with the eddy covariance technique, a technique whose underlying theory is underpinned by the assumption that all atmospheric transport is affected by turbulent surface–atmosphere exchange. To eliminate possible bias in the data introduced under conditions when the technique reaches its measurement limits, night-time NEE is thus commonly investigated using parameters representing atmospheric turbulence, like windspeed or friction velocity (u^*, Figs. 2A and B) (e.g. Fan et al., 1995; Goulden et al., 1996a; Arneth et al., 1998b; Hollinger et al., 1998; Aubinet et al., 2000; Falge et al., 2000).

Half-hourly night-time fluxes at Zotino varied typically between average values around 0.5 μmol m^{-2} s^{-1} during spring and autumn and values of up to 2.5 μmol m^{-2} s^{-1} during summer (Figs. 1A–C and 2A). At Fyodorovskoye shortly after snowmelt in late March (Kurbatova et al., 2002) night-time NEE were similar to rates measured at Zotino (Figs. 1E and 2B). However, during summer average respiration at Fyodorovskoye was higher than at Zotino, sometimes reaching values greater than 3 μmol m^{-2} s^{-1}. At both bogs the scatter in the night-time data that was observed both as positive and negative values increased measurably when the friction velocity was lowest (Figs. 2A and B). Notably, a similar relationship between night-time NEE and friction velocity was also found at a bog in Canada (Lafleur et al., 2001); it differs
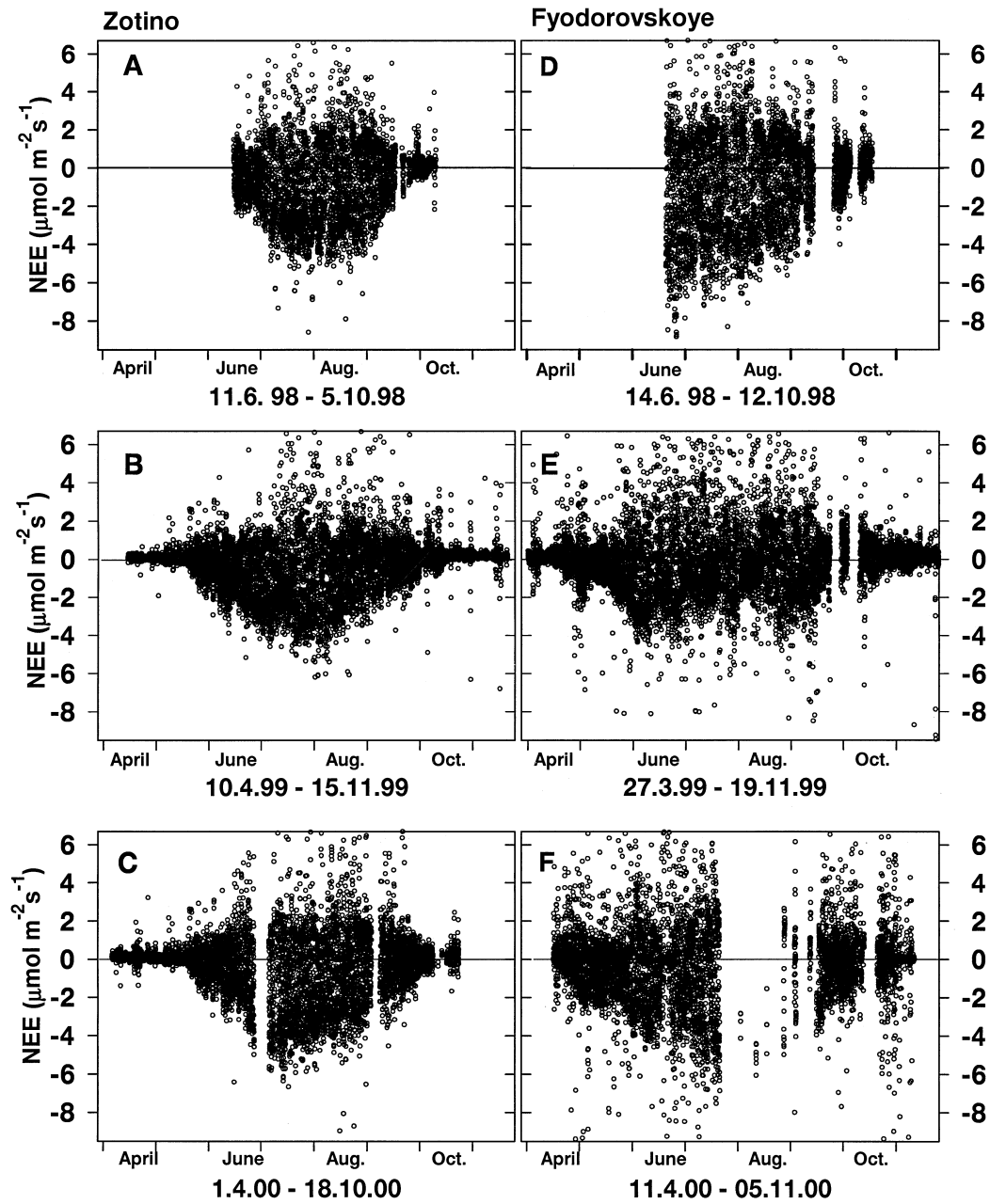
Fig. 1. Half-hourly net ecosystem CO_2 fluxes (NEE) measured at a central Siberian (Zotino, A–C) and a European Russian (Fyodorovskoye, D–F) bog measured during three vegetation periods by the eddy covariance technique.

from typical forest data where measured fluxes tend to uni-directionally decrease at low windspeed (e.g. Fan et al., 1995; Goulden et al., 1996b; Aubinet et al., 2000; Milyukova et al., 2002; Tchebakova et al., 2002).

At neither of the two sites did the pattern change seasonally or between years and, based on Fig. 2, single u^*-thresholds were selected below which night-time flux data were excluded from further analysis. At

Table 1. *Monthly climate and carbon exchange at the two sites during the months June–September*[a]

	T_5, °C	Q, mol m^{-2} month^{-1}	P, mm	R_{10}, μmol m^{-2} s^{-1}	R, mol m^{-2} month^{-1}	NEE, mol m^{-2} month^{-1}	GPP, mol m^{-2} month^{-1}	GPP/Q, mmol mol^{-1}
Zotino								
1998 - 6[b]	12.3	723.3	30.0	0.72	1.63	−0.18	2.4	3.6
- 7	17.1	1382.2	10.1	0.78	3.94	−3.01	6.9	5.2
- 8	15.8	890.5	73.0	1.04	4.36	−1.28	5.6	7.2
- 9	7.3	345.3	66.1[c]	0.78	1.47	0.21	1.3	3.9
1999 - 4	−0.5	761.8	n.a.[c]	0.32	0.16	0.15	0.01	0.01
- 5	8.6	1090.3	20.5[c]	0.84	1.26	−0.23	1.49	1.50
- 6	10.4	1045.2	47.3	0.91	2.39	−1.93	4.32	4.65
- 7	17.9	1289.2	39.2	0.88	4.70	−1.71	6.41	5.48
- 8	12.6	795.4	66.2	0.92	3.06	−0.96	4.02	5.53
- 9	6.4	539.4	15.5	0.90	1.76	0.35	1.41	3.10
- 10	n.a.	244.8	25.9[c]	0.81	0.77	0.54	0.25	1.01
2000 - 4	5.6	847.5	n.a.[c]	0.44	0.33	0.29	0.05	0.06
- 5	9.3	1118.7	49.0[c]	0.79	1.32	−0.05	1.37	1.47
- 6	16.9	1184.2	73.2	0.73	3.57	−1.97	5.54	5.16
- 7	16.3	1220.3	29.6	0.94	5.34	−3.03	8.37	7.65
- 8	15.4	828.4	46.2	0.96	4.02	−0.79	4.81	6.25
- 9	8.0	446.9	49.4[c]	0.93	2.12	0.33	1.78	4.50
Fyodorovskoye								
1998 - 6[b]	16.6	612.6	39.9	1.15	2.46	−1.89	4.72	8.37
- 7	17.1	980.9	181.1	1.21	6.10	−2.07	8.17	9.20
- 8	15.0	748.6	123.4	1.13	4.84	−1.11	5.95	8.84
- 9	14.7	261.3	50.7	0.85	2.14	−0.11	1.87	6.30
1999 - 4	5.9	786.8	20.5	0.75	1.54	0.36	1.17	1.53
- 5	8.1	1077.2	26.4	0.86	2.01	−0.89	2.9	2.88
- 6	17.4	1400.5	30.9	1.12	5.59	−0.45	6.05	4.39
- 7	18.7	1281.9	47.6	1.15	5.53	0.89	4.69	3.98
- 8	14.5	835.1	116.2	1.28	4.53	0.67	3.81	5.26
- 9	10.9	595.6	25.8	1.23	2.76	0.5	2.26	4.73
- 10	5.5	203.6	86.5	1.18	1.52	0.71	0.74	4.68

[a]The climate data are monthly average soil temperatures at 5 cm depth (T_5), total photon flux density (Q), and precipitation (P). Carbon fluxes are given as average night-time R_{10} (for definition see text), total ecosystem respiration (R) and 24 h CO_2 fluxes (NEE). GPP is the difference between NEE and R; as it denotes a productivity it is given with a positive sign. In 2000, complete data were only available for the Zotino site.
[b]Measurements started on 11 June in Zotino and on 14 June in Fyodorovskoye.
[c]Only rainfall data as the raingauge was not heated.

the Zotino bog, this threshold was taken as 0.055 m s^{-1}, while at Fyederovskoye the value was slightly higher at 0.06 m s^{-1}. At both sites taking this threshold as a criterion for reliable night-time flux data removed most, but not all, of the dubiously high or low fluxes.

For the remaining data a clear trend of night-time NEE increasing with temperature was apparent (Figs. 3A and B) with the relationship as described by the modified Arrhenius function of Lloyd and Taylor (1994) using 5 cm soil depth temperatures. The choice

of the appropriate soil depth for temperature measurements in such relationships must be somewhat subjective. We note that in ecosystems, particularly where the above-ground biomass is relatively small, roots and heterotrophic organisms dominate respiration. Root density declines exponentially with depth (Jackson et al., 1996), as does microbial activity, and thus soil temperature appropriately integrated with depth should be used. The microtopography in the bog ecosystems under study was very heterogeneous and the general appearance of the bog's surfaces did
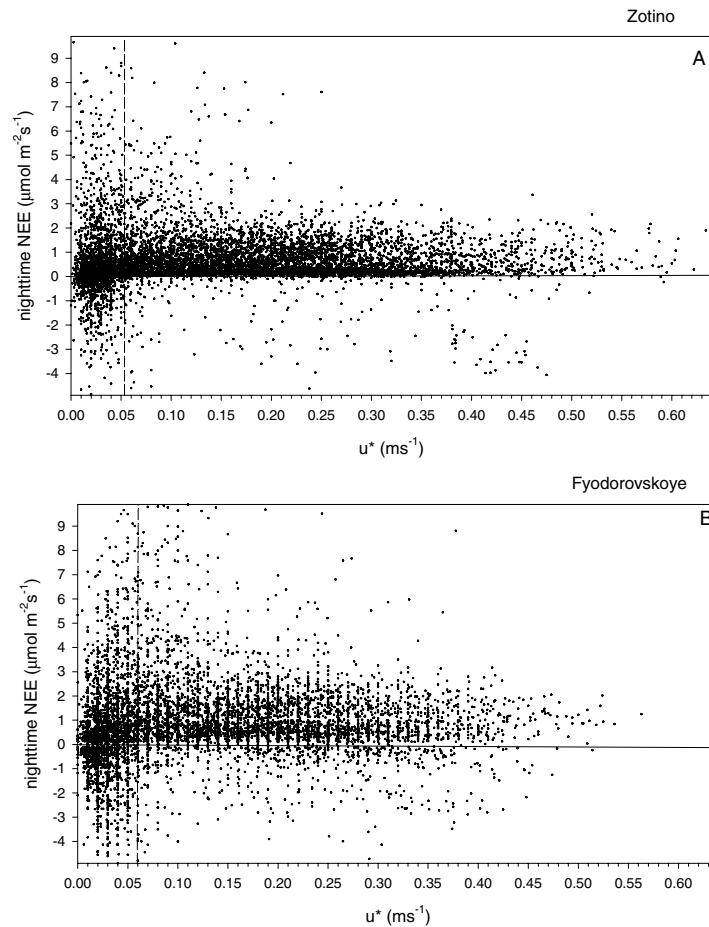
Fig. 2. Night-time NEE as a function of atmospheric turbulence (expressed as friction velocity, u^*) at Zotino (A) and Fyodorovskoye (B). Data are from all three measurement periods. The vertical lines show the u^*-thresholds below which data were considered doubtful and excluded from the data set. The threshold value at any of the two sites did not differ between years.

change rapidly throughout the year as water level dropped below the surface (Kurbatova et al., 2002). Consequently, soil surface and near-surface temperatures could not be measured satisfactorily, and we had to resign using 5 cm soil depth measurements to investigate the variability in the measured nighttime fluxes (Fig. 3).

By fitting the Lloyd and Taylor model to the data, the respiration rate at a reference temperature (e.g. 10 °C), R_{10}, is determined. This parameter allows comparison of the seasonality of respiration rates as well as a comparison of interannual variability or the comparison between sites. For the entire data set at Zotino, R_{10} values varied between 0.95 and 0.98 μmol m^{-2} s^{-1} for the

three measurement years, and consequently a single fit is shown in Fig. 3A. At Fyodorovskoye, values of R_{10} were between 1.03 in 2000 and 1.2 μmol m^{-2} s^{-1} in 1998. The somewhat higher R_{10} at Fyodorovskoye in the 1998 data might reflect that these were restricted to more or less the period of highest activity when soil temperatures were already warm (see below). Overall, respiration at 10 °C was 10–20% higher at Fyodorovskoye than at Zotino (Fig. 3, Table 1).

While R_{10} for the full-length data sets were generally consistent, values varied somewhat periodically throughout the year. This can also be observed in Fig. 3, where the fit through the data tends to overestimate ecosystem respiration rates at lower
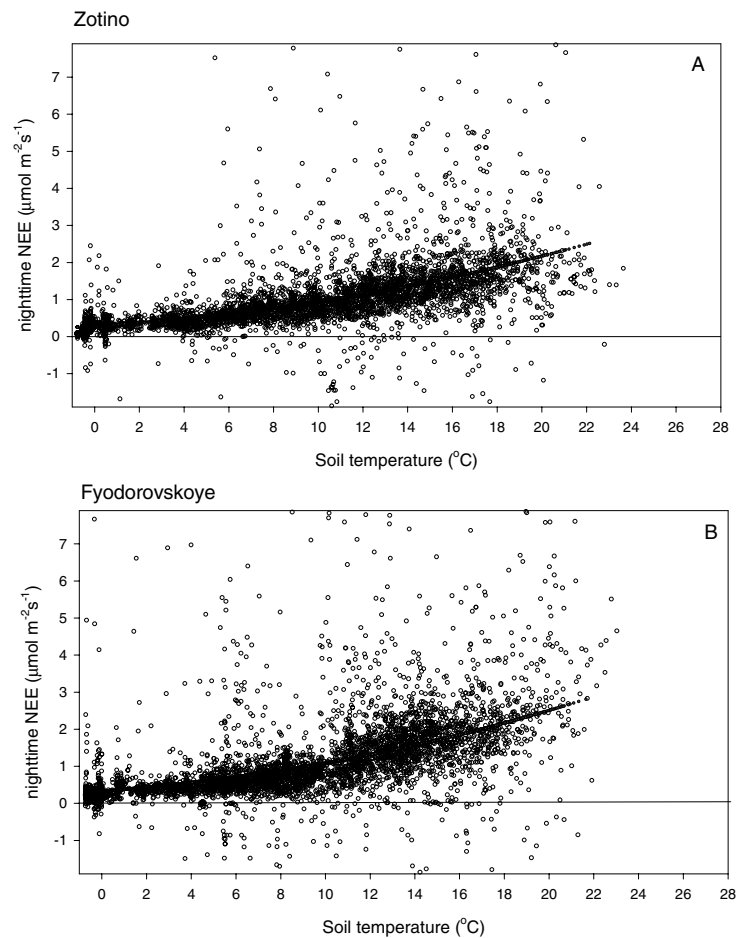
Zotino

Fyodorovskoye

Fig. 3. The relationship between nighttime NEE fluxes and peat temperature in 5 cm depth at the two bog ecosystems. Data were measured during periods when $u^* > 0.055$ (Zotino, A) or $u^* > 0.060$ (Fyodorovskoye, B). There was no significant difference in the temperature response between years. The lines are fits through the data using the Lloyd and Taylor soil respiration model.

temperatures. When data were grouped into monthly bins average R_{10} were lowest in spring (Table 1) and increased rapidly towards summer. The seasonality was exceptionally strong in the Zotino data set, where R_{10} between spring and summer varied by a factor of three, likely the combined effect of a decreasing water table, increasing temperatures and increasing productivity: in wetlands, a drop in water table allows aerobic decomposition to take place and also advocates oxygen supply to the roots of vascular plants. Respiration rates under these conditions tend to increase (Armentano and Menges, 1986; Moore and Dalva, 1993; Alm et al., 1999). We did not measure water table depth at our study sites, but the free water surface area was observed to decline considerably as daily summer evaporation rates consistently exceeded precipitation. This is quantifiable by relying upon a simple bucket monthly (*t*) water balance as $\Theta_t = (\Theta_{t-1} + P - E)$, where Θ is peat moisture content, *P* is precipitation, *E* is evaporation (Kurbatova et al., 2002) and Θ_t is normalised to an assumed maximum peat water storage of 200 mm over a depth of 250 mm. Surplus precipitation is assumed to drain to deeper depths. For the growing season months (May–September) R_{10} at Zotino increased linearly as surface Θ were estimated to decline from 1 to 0.4 ($y = -0.26x + 1.06, r^2 = 0.25$).

This relationship, based as it is on a quite simplified analysis, is weak. Naturally the thawing and gradual warming of peat and water in deeper soil layers also played a role in the increase of R_{10}. In tundra soils, respiration rates at a reference temperature increased considerably when soils at sub-zero temperatures were compared to soils at 5 °C (Clein and Schimel, 1995). Our data thus may indicate a shift from microbial maintenance to growth respiration as well as a change in population density and structure, in combination with increasing root respiration as vascular plants develop over the course of the season.

For the Fyodorovskoye data the question now arises however why, firstly, R_{10} were higher than in Zotino and, secondly, why R_{10} did not vary as strongly seasonally: R_{10} in April and May were about 75% of summer values. In fact, monthly evaporation does not exceed precipitation on a regular basis in the Fyodorovskoye bog (Kurbatova et al., 2002) and Θ does not vary as much. This leads us to speculate whether seasonal variation in R_{10} at Fyodorovskoye may be mostly associated with plant growth and microbial activity patterns. The generally higher R_{10} in that case tell of a deeper active peat layer as the soil warms to a deeper depth, and perhaps also higher plant biomass turnover (which may lead to larger labile carbon pools)

although there are no data available to assist this suggestion.

Instantaneous daytime fluxes

Just as for the night-time fluxes, at both sites a strong seasonality in NEE during daylight hours was observed. Daylight NEE before snowmelt [early May at Zotino and mid-April at Fyodorovskoye (Kurbatova et al., 2002)] were positive but small, <0.5 μmol m^{-2} s^{-1} at both sites (Fig. 1). Photosynthesis then commenced rapidly as indicated by negative daylight NEE. During summer minima around -4 to -5 μmol m^{-2} s^{-1} at Zotino and around -6 to -7 μmol m^{-2} s^{-1} at Fyodorovskoye were attained. Notably, at Fyodorovskoye, daylight minima during the dry and warm summer 1999 were only slightly below -4 μmol m^{-2} s^{-1}. At Zotino, daylight fluxes during early July 2000 were more negative than at any period during 1998 and 1999 (see later discussion).

Figure 4 illustrates the hyperbolic relationship that generally existed between NEE and quantum flux density (Q), by plotting selected five-day periods in early spring (May), early summer (July) and early autumn (September) 1999. At both sites, the response of daytime CO$_2$ uptake to incoming quantum flux increased rapidly after snowmelt. This increase in sensitivity
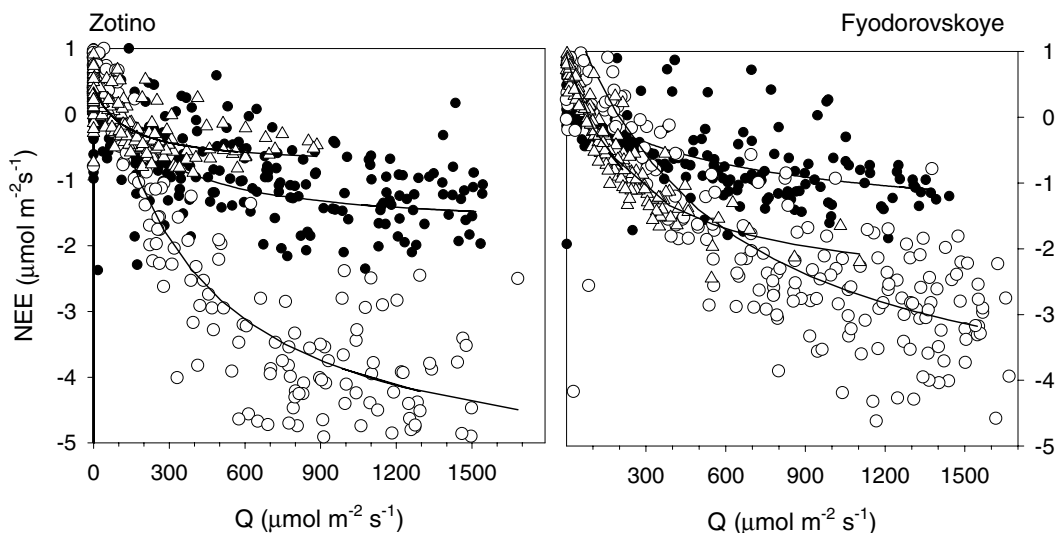

Fig. 4. Light response of NEE during three example five-day periods at both sites. Data are from measurements during early spring (May, closed circles), early summer (July, open circles) and late autumn (September, open triangles) 1999. Lines are hyperbolic fits through the data.

towards Q was accompanied by increasing temperatures (Table 1) and a decrease in free water surface. A general 'greening' of the bog's surfaces as the mosses develop new chlorophyll and the herbaceous vegetation grows new leaves could also be seen from an increased albedo (in our case from daytime average of ca. 13% after snowmelt to ca. 20% by the end of July (Kurbatova et al., 2002; Nichol et al., 2002). The pattern was reversed in autumn, when the slope of the relationship between the rate of net uptake of CO_2 and Q was lower than in summer, also tending towards saturation at lower PAR. The observed plasticity clearly demonstrates that for regional or global modelling of productivity in northern wetlands a pronounced seasonality in ecosystem photosynthetic capacity needs to be taken into account.

Rates of NEE observed during the height of the growing season in this study were noticeably more negative than CO_2 fluxes measured at most other boreal bog ecosystems (Neumann and den Hartog, 1994; Waddington and Roulet, 1996; Bellisario et al., 1998; for a review see Frolking et al., 1998). For example, at Fyodorovskoye, maximum uptake during summer was only insignificantly below rates considered to be more typical for higher productivity fens (Frolking et al., 1998). The degree to which a potential bias due to measurement techniques has to be considered here is uncertain. Most studies on carbon fluxes in boreal bogs have been conducted using chamber techniques. To date only few studies have directly compared chamber and eddy flux measurements; based on these there may be general disagreement between chamber and micrometeorological techniques (Nay et al., 1994; Arneth et al., 1998a). The reasons for discrepancies between the techniques are manifold, one major problem of chamber techniques is the distortion of diffusion and/or pressure gradients that exist between the soil pores and the atmosphere. In bogs an additional difficulty is introduced by the highly variable microtopography. Fluxes measured in 'hollows' or 'ridges' may differ by magnitudes, some microsites within the same wetland have shown to be sources, others were sinks for CO_2 (Waddington and Roulet, 1996; Alm et al., 1999; Christensen et al., 2000). This complicates the upscaling of chamber data. For ombrotrophic bogs we are only aware of three eddy flux studies (Neumann and den Hartog, 1994; Valentini et al., 2000; Lafleur et al., 2001). From these one was in the vicinity of the Zotino site, and maximum CO_2 uptakes during July were scarcely higher (Valentini et al., 2000). The other boreal bog site, located in Canada, had a

lower mid-day uptake [-3.5 to -4.5 μmol m^{-2} s^{-1}; (Neumann and den Hartog, 1994)]; however, there were some indications of surface drying reducing summer NEE. In a second Canadian bog, located in a temperate climate area summer maximum uptake was up to -8 μmol m^{-2} s^{-1}.

Gap filling

Based on the described relationships of night NEE with u^* and temperature (Figs. 2 and 3) a standard procedure of gap-filling was developed which allowed the calculation of data that were either missing because of instrument failure or that were excluded because of the applied u^*-threshold. Using a Fortran routine (Kolle, unpublished), gaps of two hours or less were spline-interpolated by an Akima spline function. Longer periods of missing or excluded data were filled using the Lloyd and Taylor model applying an average R_{10} that was calculated from 1400 data points, thus allowing for the observed seasonality in R_{10}.

In a process similar to the night-time data, short gaps of 2 h or less during daylight hours were interpolated by a spline procedure. Longer periods were filled by fitting a hyperbolic light response of the form $y_0 + ax/(b + x)$, whereby 100 data points before and after each gap were used as input in the fitting routine. Thus the observed seasonal change in the NEE-light response was accounted for. For the fitting, the data were grouped into quantum flux density (Q) classes of 100 μmol m^{-2} s^{-1}; using a Fortran routine we compared the goodness of fit for a Simplex as well as a Levenberg–Marquhardt algorithm to determine the parameters required to describe the hyperbola (Kolle, personal communication). The parameter values and the goodness of fit between the measured and the fitted data were in most cases identical.

24 h NEE and data

Figure 5 compiles daily Q, average soil temperatures and daily NEE for the three observation periods at both sites. Table 1 additionally includes monthly sums of total ecosystem respiration and ecosystem GPP (derived as the difference between NEE and R; given with a positive sign). The calculation of R included estimation during daylight hours using the Lloyd and Taylor model with changing average monthly R_{10} values (Table 1). Mitochondrial respiration in green tissue of vascular plants is reduced during daylight hours (Brooks and Farquhar, 1985), and the same situation may hold for bryophytes. In estimating daytime
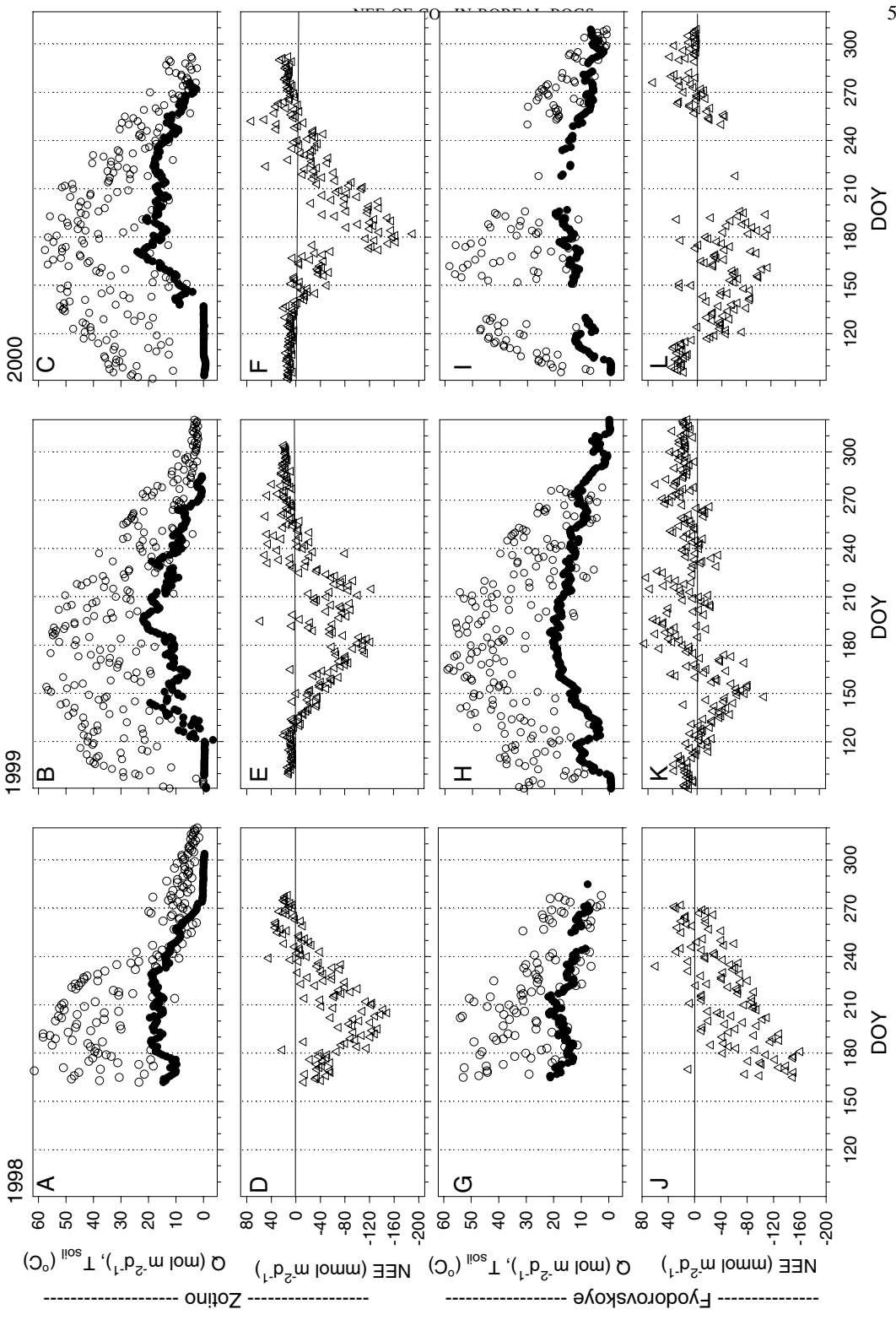
Fig. 5. Daily quantum flux density (*Q*, open circles) and soil temperatures (*T*soil, closed circles; Zotino, A–C; Fyodorovskoye, D–F; Fyodorovskoye, G–I), and 24 h NEE (Zotino, D–F; Fyodorovskoye, J–L).

respiration then, as we have used the night-time relationships of Fig. 3, we also acknowledge that we may have overestimated daily respiratory totals somewhat.

Overall, total daily NEE at Zotino varied between values of ca. +20 in spring before snowmelt and maximum rates between −120 and −190 mmol m^{-2} d^{-1} during the summer months (Fig. 5). Daily Q (and air temperatures, not shown) before and during snowmelt were already significant (up to 50 mol m^{-2} d^{-1}), but isolation by the snowcover kept soil temperatures just below zero, without day-to-day variation. Accordingly, scatter in NEE was also marginal. The transition from net loss to net uptake took place rapidly within a period of only few days. In summer, soil temperatures warmed to 20 °C, while Q on clear days were ca. 55 mol m^{-2} d^{-1}. The bog reverted from net uptake to a net loss between late August and September (doy 230–270). The changeover of NEE was accompanied by Q declining rapidly as daylength and sun angle decreased, but soil temperatures at 5 cm depth remained above zero until first snowfall.

At Fyodorovskoye, NEE varied seasonally between ca. 40 mmol m^{-2} d^{-1} in spring and autumn and −120 and −160 mmol m^{-2} d^{-1} during summer 1998 and 2000. Average NEE measured on five days that showed the highest net uptake rates in 1998 were −152 mmol m^{-2} d^{-1}, somewhat less than rates measured on five days with the highest net uptake rates at Zotino (−166 mmol m^{-2} d^{-1} in 2000). The spring transition from net carbon loss to net carbon uptake took place in 2000 about one month earlier, but in 1999 only few days earlier, than at Zotino. Net fluxes became positive in autumn around early to mid-September; the similarity in autumnal decline of CO_2 uptake in Fyodorovskoye and Zotino confirmed the strong influence of decreasing Q and temperature, and consequently plant senescence, on carbon uptake at both sites (Fig. 4). In 1999 the seasonal pattern was distinct, as net carbon uptake was only observed during a brief period in May and June. From late June onwards, the system was a significant source of carbon on most days.

At Zotino, the autumnal sink–source transition period was characterised by originally relatively large carbon losses before, by the end of September, values settled around 10–20 mmol m^{-2} d^{-1}. It appears that the relatively rapid decline of NEE > 20 mmol m^{-2} d^{-1} to NEE < 20 mmol m^{-2} d^{-1} in autumn was related to the onset of first frosts during this time (Kurbatova et al., 2002) as respiration rates in soils are known to

decline rapidly at sub-zero temperatures (Clein and Schimel, 1995). It was not caused by snowfall per se because in 2000 first snow did not fall until mid-October. At Fyodorovskoye, where soil temperatures remained warm until early November and where first snowfall occurred not before mid–late November, a similar sharp drop in NEE was not observed (Fig. 5). There the observed NEE in autumn before measurements ceased and in spring just after measurements commenced were similar.

At both bogs a distinct interannual variation in seasonal carbon fluxes was observed. We believe that these were largely related to dry and warm weather conditions. The most visible episode was the shift in NEE from net uptake to a net loss during summer 1999 at Fyodorovskoye (Fig. 5K). At Zotino there also was a strong decline in carbon uptake in summer 1999, albeit during a much shorter period (Fig. 5E). Coincidentally, at both sites climate was warm and dry during this year. This was particularly so for Fyodorovskoye, where June and July precipitation was well below the long-term average. A second period of interest was evident in 2000 during late June/early July (doy 170–190, Fig. 5F) when NEE at Zotino exceeded uptake during the other years by far (NEE ≤ −160 mmol m^{-2} d^{-1}).

As discussed above, in bog ecosystems a drop in water table significantly increases respiration rates (Funk et al., 1994; Alm et al., 1999) because of the increased oxygen availability for microbial decomposition and root growth. At the two bogs studied here there was some indication that R_{10} were higher in the dry periods, at least for the Zotino site, but differences are hard to detect because of the inherently high scatter in the eddy flux data. Additionally, water table and soil temperature interact, e.g. dry soils warm faster than wet soils. Respiration rates during were consequently large during warm and during dry summers (Table 1).

The relatively small changes in ecosystem respiration between dry and wet years led to the deduction of a generally large effect of surface dryness on ecosystem GPP, e.g. reduced photosynthesis of both vascular plants and the *Sphagnum* mosses contributed noticeably to the observed reduction in NEE. In Fig. 6, the relationships between daily GPP and Q for a below-average dry and an average wet summer are shown (at Zotino, 1999 and 2000; at Fyodorovskoye, 1999 and 1998) are shown. For both sites that data demonstrate the distinct shift in the sensitivity of ecosystem carbon uptake towards Q that takes place throughout the year. This had also been seen in diurnal NEE data (Fig. 4). However, what is of more importance is how
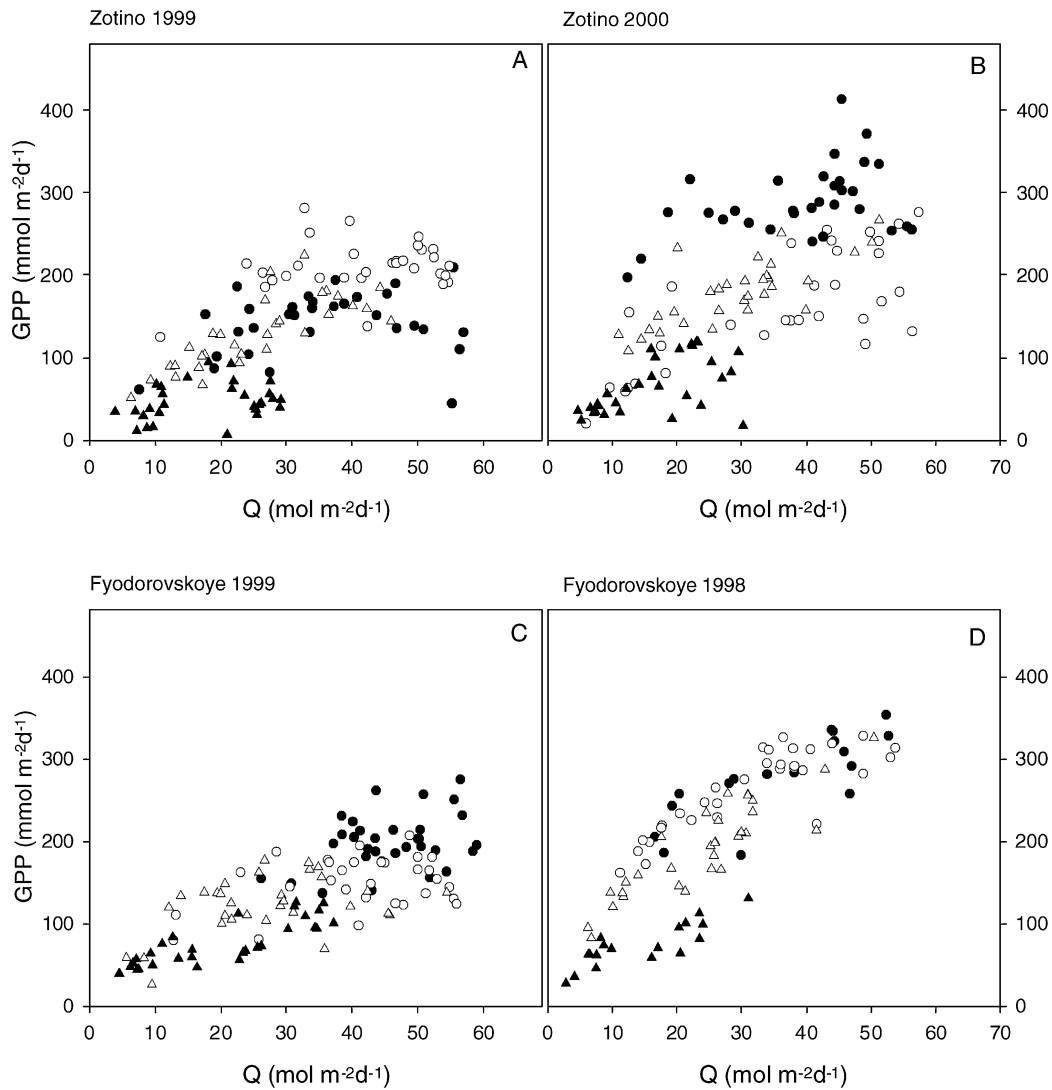
Fig. 6. Ecosystem GPP vs. *Q* during the summer months. The data represent below-average dry periods (1999) and average wet periods (1998 at Fyodorovskoye and 2000 at Zotino). The data are grouped into monthly bins where June = filled circles, July = open circles, August = open triangels, September = filled triangles.

during the dry months at both sites (1999) GPP at a given *Q* was clearly reduced below values during normally wet months (1998 at Fyodorovskoye and 2000 at Zotino).

Our data confirm observations found for a variety of northern ecosystems. Mosses are generally able to tolerate water stress relatively well (Skre and Oechel, 1981) and in *Sphagnum* lawns at a Finnish bog photosynthesis rates remained at a high level despite a sig-

nificant drop in water table during dry summer conditions (Alm et al., 1999). However, photosynthesis rates were greatly reduced in desiccated mosses growing on hummocks. Some of the reduction was irreversible after rewetting, indicating a permanent damage to the photosynthetic tissue. In *Sphagnum* and other moss species growing within taiga forests of Alaska, a similar response of photosynthesis to desiccation and rehydration was found (Skre and Oechel, 1981). At

Fyodorovskoye, NEE recovered somewhat after rainfall rewetted the surface in mid-August (Fig. 5K, doy > 220). At Zotino, NEE increased rapidly to rates > -80 mmol m^{-2} following a 30 mm rain event (Fig. 5E, doy 200–210). These data suggest a limitation of NEE by reduced photosynthesis at consistently high respiration during dry periods, which in the case of photosynthesis is at least partially reversible.

The increase in total CO_2 uptake in spring 2000 from values >0 to maximum uptake rates happened extraordinarily rapidly at Zotino (Fig. 5F). Within only one day, fluxes changed from values around -40 mmol m^{-2} d^{-1} to values < -100 mmol m^{-2} d^{-1}, and were approximately 40–50 mmol more negative than in 1998 and 1999. Without detailed modelling analyses (which are beyond the scope of this paper) it cannot be ascertained which factors precisely controlled the sharp increase in carbon uptake. Due to a spell of cool temperatures respiration over that period dropped; however, they were not different, for example, from rates in 1999 during the same period (not shown, but see Table 1). Summer 2000 at Zotino was relatively wet and precipitation was distributed more evenly (Kurbatova et al., 2002). This may be of importance as *Sphagnum* photosynthesis responds to water content in an optimality function, i.e. it declines below and above a certain hydration level (ca. 7 $g_{freshweight} g_{dryweight}^{-1}$) (Williams and Flanagan, 1996). During July 2000 GPP at a given Q were higher than during any other month at Zotino (Fig. 6B). Most likely cool temperatures (low respiration) at a high radiation

level and adequate moisture supply (high GPP) will all have contributed to the observed pattern of NEE.

Total NEE during the observation period at Zotino were -3.6 mol m^{-2} in 1999 and -5.0 mol m^{-2} in 2000. Cumulative NEE in 1999 and 2000 could be compared more or less directly because measurements commenced only 10 days apart (1 and 10 April), when fluxes were still very low (Fig. 7). Taking commencement of the measurements as a starting point, the bog started accumulating carbon late May 1998 (doy 148), and nearly 2 weeks later in 2000 (doy 161). The delay in the onset of net carbon accumulation in 2000 was not the result of the earlier start of measurements (when fluxes were still positive) but due to longer snowcover that excluded photosynthesis (Figs. 5E and F). However, despite the delay in the onset, net uptake 'accelerated' in 2000, the possible reasons for which have been discussed above. Total uptake that was observed during the 200 days of measurement was nearly 40% higher compared to the 220 days of measurement in 1999. Uptake from mid-June 2000 onwards also exceeded uptake in 1998 during the same time period (-4.8 mol m^{-2}). The picture at Fyodorovskoye was completely different: while uptake in the 107 day period in 1998 was nearly similar to uptake at Zotino (-5.2 mol m^{-2}, Fig. 7), the dry climatic conditions during 1999 gave rise to the bog being a source of carbon; for the entire season NEE totalled 2.2 mol m^{-2}.

Interestingly, based on ^{14}C dating, Turunen et al. (2001) found that accumulation rates in west Siberia were similar to bogs from much colder climates. This
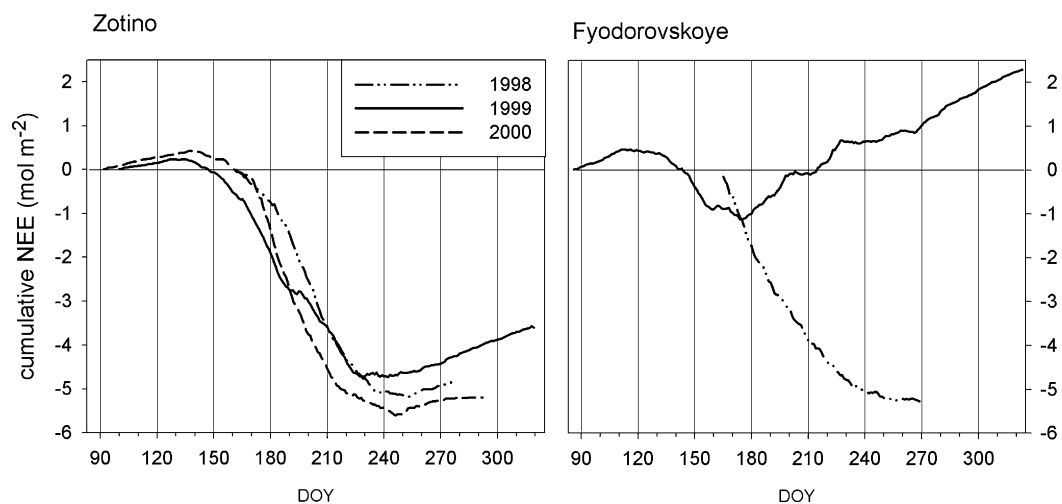

Fig. 7. Cumulative NEE at Zotino (A) and Fyodorovskoye (B).

picture fits with our results for climatically average years in Zotino and Fyodorovskoye. On the other hand, in an extensive study over a subarctic fen NEE during a summer 75-day period in five different years varied between -5.3 and 1.7 mol m^{-2} (Griffis et al., 2000). For this site, too, the authors concluded that it was variation in photosynthesis, not in respiration, that contributed most to the interannual differences. In two boreal fens located in Canada, CO$_2$ uptake between mid-May and early October was -7.3 mol m^{-2} at the more northern site and 2.5 mol m^{-2} between early April and mid-September at the more southern site (Lafleur et al., 1997; Suyker et al., 1997). At a wetland in north-central Minnesota, climate in a wet and cool growing season also promoted C uptake (-2.6 mol m^{-2} between May and October), while warmer and drier conditions resulted in the wetland losing carbon (Shurpali et al., 1995). The data suggest that CO$_2$-C fluxes in northern wetlands vary considerably with respect to weather conditions and that in dry years the systems are prone to loose carbon.

Uncertainties associated with the total CO$_2$ uptake during the measurement period

At both sites, between 10 and 15% of the total half-hours during the measurement periods needed to be estimated either because of instrument failure or because of exclusion of the original data after applying the u^*-threshold. By treating the data in such a way a bias due to measurement limitations at high atmospheric stability is removed, but of concern is the introduction of another bias through the gap-filling procedure (Falge et al., 2000). Any bias will accumulate, the more the longer the data integration period. Random errors associated with instrumentation accuracy, in contrast, will diminish (Moncrieff et al., 1996). For the periods studied, at Zotino the corrected, gap-filled fluxes were -4.8, -3.6 and -5.0 mol m^{-2} during the three measurement periods 1998, 1999 and 2000. At Fyodorovskoye, cumulative fluxes were only calculated for 1998 and 1999 and were -5.0 and 2.2 mol m^{-2}, respectively. At all sites these sums were more positive when compared to the sums calculated using the original eddy flux data, i.e. without applying the gap-filling criteria and exclusion of data at low u^*. This implies that despite the bidirectional scatter in NEE at low u^* (Fig. 2), there was a tendency for data being below night-time averages at high stability. Nevertheless, with the exception of the 1999 Fyodorovskoye data, total CO$_2$ uptake calculated after

applying the u^* threshold was within 15% of the 'eddy' sums calculated without applying the threshold. We thus associate at a first instance an uncertainty of -15% with the carbon uptake totals given above.

At Fyodorovskoye in 1999, however, the uncertainty is much higher. The uncorrected eddy data suggested a cumulative NEE of -0.2 mol m^{-2}. The large difference between the data before and after applying the threshold criterion reflect the warm temperatures during this particular summer period. As a consequence, replaced values were generally $>25\%$ above the original values, which over the vegetation period accumulated to a difference of ca. 2.2 mol m^{-2}.

Do our data allow an estimate of annual CO$_2$-C exchange? We believe it does: at the very least it allows one to put erudite constraints on annual rates, particularly for 1999 and 2000 at the Zotino site. The data suggest constant, low CO$_2$ fluxes before the onset of snowmelt in spring, and again constant but somewhat higher fluxes after first snowfall in autumn, when soil temperatures were still warm and uncompressed snow allowed easy diffusion of CO$_2$ (Fig. 5). Average fluxes measured during 14 days in early spring and in autumn were 12.5 ± 5.4 and 12.1 ± 4.4 mmol m^{-2} d^{-1} in 1999 and 2000, respectively. Applying these spring and autumn averages to the 145 and 165 (winter) days of the year not covered by measurements gives an estimated winter loss of 1.8 mol m^{-2} (145×12.5) mol m^{-2} in 1999 and 2.0 mol m^{-2} (165×12.1) in 2000, supporting the view that winter carbon loss in boreal wetlands is significant despite the small instantaneous rates (Oechel et al., 1997; Panikov and Dedish, 2000; Laurila et al., 2001). Combined with summer data annual carbon uptake in the Zotino bog in 1999 was then -1.8 mol m^{-2}, and in 2000 it was -3.0 mol m^{-2}. At Fyodorovskoye average daily NEE during 14 days in early spring 1999 was 16.2 ± 7.1 mmol m^{-2}, or 2.1 mol over 128 winter days. For 2000 and 1998 these calculations could not be repeated because of the large part of the vegetation period that was not covered by measurements. We associate with the annual values a relatively small random error of perhaps ± 10–15% (Moncrieff et al., 1996) but, as described above, a uni-directional 15% uncertainty originating from the data treatment.

4. Conclusion

Our data confirm the expected modest but significant net carbon uptake in boreal bog ecostems

during climatically average years. As has been shown before for boreal forest ecosystems seasonal and interannual climate variability has a pronounced impact on the magnitude and also on the direction of the integrated CO_2-C fluxes. Our data indicate a strong seasonality in NEE, with maximum summer activity being both the result of maximum microbial and root respiration when water tables are low and of maximum photosynthetic capacity when temperatures are warm and ecosystem chlorophyll content is highest. Interannual differences, however, were only to a minor degree caused by differences in respiration; variations in precipitation and bog water table affected annual carbon uptake mainly via plant carbon assimilation.

It should be kept in mind that our analysis does not represent a complete carbon balance: We have not considered other important carbon fluxes (e.g. methane, DOC runoff). These fluxes may significantly reduce total carbon uptake in northern wetlands. Moreover, from a greenhouse forcing perspective, net ecosystem CO_2-C uptake may be nearly completely balanced by methane production in boreal wetlands (T. Christensen, personal communication).

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