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Spring in the boreal environment: observations on pre- and post-melt energy and CO_2 fluxes in two central Siberian ecosystems

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A range of observations points towards earlier onset of spring in northern high latitudes. However, despite the profound effects this may have on vegetation–atmosphere exchange of carbon (NEE), vegetation–atmosphere physical coupling, or the location of the tundra–taiga interface, the number of studies that investigate winter–spring transition fluxes in contrasting northern vegetation types is limited. Here, we examine spring ecosystem–atmosphere energy and carbon exchange in a Siberian pine forest and mire. Divergent surface albedo before and during snow-melt resulted in daytime net radiation (R_n) above the forest exceeding R_n above the mire by up to 10 MJ m^{-2}. Until stomata could open, absorbed radiation by the green pine canopy caused substantial daytime sensible heat fluxes ($H >$ 10MJ m^{-2}). H above the mire was very low, even negative (< -2 MJ m^{-2}), during that same period. Physiological activity in both ecosystems responded rapidly to warming temperatures and snow-melt, which is essential for survival in Siberia with its very short summers. On days with above-zero temperatures, before melt was complete, low rates of forest photosynthesis (1–2 μmol m^{-2} s^{-1}) were discernible. Forest and mire NEE became negative the same day, or shortly after, photosynthesis commenced. The mire lagged by about two weeks behind the forest and regained its full carbon uptake capacity at a slower rate. Our data provide empirical evidence for the importance the timing of spring and the relative proportion of forest *vs*. mire has for late winter/spring boundary-layer growth, and production and surface–atmosphere mixing of trace gases. Models that seek to investigate effects of increasingly earlier spring in high latitudes must correctly account for contrasting physical and biogeochemical ecosystem–atmosphere exchange in heterogeneous landscapes.

Introduction

Arctic and boreal ecosystems are estimated to store up to 60% of the carbon in terrestrial ecosystems (Gorham 1991, Chapin *et al*. 2000, Hobbie *et al*. 2000, Prentice *et al*. 2001). Recent temperature increases as well as projections of warming in the northern high latitudes (Serreze *et al*. 2000, Houghton *et al*. 2001) have prompted discussion whether or not changes in climate may cause a change in northern ecosystem carbon balances, possibly increasing radiative forcing. A net release of carbon could result from a combination of melting permafrost, drying of wetlands and a stimulation of microbial carbon mineralization, with a potential to override the natural CO_2 enhancement of photosynthesis. But it has also been suggested that increasing temperatures and mineralization promote access to soil nutrients — thus increasing productivity and carbon uptake (e.g., Hobbie *et al*. 2000, Kirschbaum 2000, Santruckova *et al*. 2003).

An amplification of the seasonal cycle in atmospheric CO_2 concentration at northern stations, and an earlier CO_2 drawdown in spring was already recognized in the mid 1990s (Keeling *et al*. 1996, Randerson *et al*. 1999). Analysis of satellite derived NDVI data suggests a trend towards earlier greening in high northern latitudes (slowing down after the Pinatubo eruption) and this has been associated with the temperature response of photosynthetic activity in spring (Myneni *et al*. 1997, Zhou *et al*. 2001, Lucht *et al*. 2002). Recently, timing of snowmelt in the tundra regions of Siberia has been related to cumulative green season NDVI (Grippa *et al*. 2005). From such observations the question has arisen as to whether a longer ‘green’ season, which increases the period of carbon assimilation, should inevitably lead to higher net C uptake, and if so, which processes would govern such behaviour.

Snow-free periods in high-latitude northern ecosystems are relatively short, with a well adapted arctoboreal biota that can quickly respond to the rapid transition from very cold winters to warm and often dry, yet short, summers. It therefore appears both logical and plausible that the timing of snow-melt and soil thaw should have a significant impact on the seasonal or even annual ecosystem carbon (and water) balance. For example, early melt in Siberian forests may promote growth in the same year, attributable to either early cambial initiation and higher cambial cell division at subsequent higher temperatures in early summer, or to increased availability of soil nutrients (Vaganov *et al*. 1999, Jarvis and Linder 2000). A deciduous boreal aspen forest sequestered significantly more carbon after an early melt, responding to earlier leaf emergence (Black *et al*. 2000). In a subarctic fen located in Finland, the interannual variation of the CO_2 balance was closely related to the timing of snowmelt (Aurela *et al*. 2004). On the other hand, for an ombrotrophic bog in Canada, the annual net uptake could be similar in years with strongly varying seasonal weather and NEE, including pronounced differences in the timing of melt (Lafleur *et al*. 2003) and in a Canadian spruce forest depth and duration of soil thaw was found to increase soil organic matter decomposition and to decrease annual net carbon uptake (Goulden *et al*. 1998). In a subalpine mixed conifer forest, NEE was higher in years with late snow-melt in spring (Monson *et al*. 2005). Even for gross primary productivity, GPP, the picture appears ambiguous. In their analysis of NDVI (a surrogate for GPP), Grippa *et al*. (2005) demonstrated that the presence and magnitude of correlations between snow-melt date and snow depth, and vegetation activity differed between tundra, forest or steppe dominated areas. For deciduous forests in general the active season length alone, especially when denoted as number of days with green canopy, may not be a good predictor for net carbon uptake (White and Nemani 2003).

The importance of the surface vegetation for atmospheric composition and climate in northern ecosystems is not restricted to the carbon cycle. The mostly coniferous northern forests have low short-wave albedo even in winter and spring. Snow does not remain on the tree canopy itself for long and the dark tree crowns mask the snow-covered soil. In terms of the surface’s radiation balance a marked contrast thus exists between forests and the low vegetation of tundra or wetland ecosystems, which affects the short-term weather (Viterbo and Betts 1999, Betts *et al*. 2001b, Harding *et al*. 2001) as well as exerting an important climate feedback (Betts 2000). What is more, during times when liquid water is available, northern forests have generally lower evapotranspiration rates and higher sensible heat fluxes than tussock tundra or wetlands (for review *see* Eugster *et al*. 2000). The plant cover thus has an impact on local and regional climate via distinct surface albedo and energy partitioning (Foley *et al*. 2003). This has important implications for projections of the future climate, since pollen analyses as well as modelling studies indicate possible shifts of northern vegetation in response to warming, for instance shrub and forest expansion into areas dominated by moist tussock tundra or wetlands (Starfield and Chapin 1996, Levis *et al*. 1999, Bigelow *et al*. 2003).

Despite the postulated significance for ecology and climate, the number of studies that investigate in detail the winter–spring transition fluxes, and their interannual and spatial variation in boreal or (sub)arctic ecosystems are rather limited (e.g., Fahnenstock *et al*. 1998, Baker *et al*. 1999, Suzuki *et al*. 1999, Betts *et al*. 2001a, Bruland *et al*. 2001, Suni *et al*. 2003, Sicart *et al*. 2004). This is particularly the case for analyses that consider spring CO_2 fluxes as well as energy partitioning in contrasting vegetation types at the same time of the year and at the same location. A detailed knowledge of the processes taking place during the period of melt in contrasting vegetation types can help to constrain model results and to test whether models represent these processes correctly, which is essential when trying to pinpoint possible physical and biogeochemical feedbacks in the northern surface–atmosphere system. While in recent years progress has been made to assess and improve climate models and models of terrestrial carbon cycle by surface observations (Betts *et al*. 2001b, Sitch *et al*. 2003, Knorr and Kattge 2005), considerable uncertainty exists regarding the performance of these models in heterogeneous landscapes — which might be of particular importance in view of coupling these models.

In this study, we scrutinise the spring energy, carbon and water fluxes in two evergreen Siberian ecosystems, a mature Scots pine forest and a mire (Arneth *et al*. 2002a, Kurbatova *et al*. 2002, Lloyd *et al*. 2002a, Shibistova *et al*. 2002a). Flux data were measured using the eddy covariance technique in 1999 and 2000, two years that differed greatly in spring weather pattern, and in the timing and duration of snow-melt. Our analysis provides a combined "physical" and "physiological" view on the environmental control and synchronisation of the onset of photosynthesis and evapotranspiration for these two ecosystems. It presents field evidence for the effect the contrasting vegetation has on energy partitioning and CO_2 exchange during this crucial period of the year that is undergoing rapid changes.

Methods

The study area is located in central Siberia, approximately 30 km from the western bank of the Yenisey river and the small village of Zotino. The two sites and the eddy flux measurements have been described in detail elsewhere (e.g., Arneth *et al*. 2002a, Shibistova *et al*. 2002a, Tchebakova *et al*. 2002) and we repeat a brief outline only: The forest (60.75°N, 89.39°E) is relatively simply structured with a single canopy layer of even aged ca. 22-m-tall *Pinus sylvestris* that were 200 years old when the measurements commenced in 1998. Herbaceous understorey is virtually absent apart from patches of *Vaccinium* ssp.; most of the ground is covered by lichen. The mire (60.76°N, 89.41°E), located within only a few hundred metres of the forest site is dominated by *Sphagnum*-peat hollows which were partially inundated throughout the snow free season, and ridges also formed by *Sphagnum* ssp. but with a variety of herbaceous plants and crummy pine trees growing atop. The two adjacent ecosystems are typical of the vegetation dominating the latitudinal band between ca. 58°N and 64°N to the west of the Yenisey river (Kalaschnikov 1994). The climate of the area is continental with low mean annual air temperatures and precipitation (–1.5 °C, 590 mm). About 50% of the precipitation falls as snow. Summers are generally warm, and as average temperatures in July are close to 20 °C substantial air saturation and soil moisture deficits can develop to be characteristic constraints to carbon and water fluxes (Kelliher *et al*. 1998, Arneth *et al*. 2002b, Lloyd *et al*. 2002a, Shibistova *et al*. 2002b).

In June 1998 at each of the two sites one eddy covariance tower was instrumented to measure fluxes of energy, carbon and water. The set-up followed closely that described by Aubinet *et al*. (2000). In short, it consisted of a three dimensional sonic anemometer (Solent R3, Gill Instruments, Lymington, UK) located well above the canopy for measurements of fluctuations in wind speed and virtual air temperature in combination with a closed-path infrared gas analyser (LI-COR 6262, Lincoln, USA) located at the bottom of the tower to measure water vapour and CO_2 mixing ratios. Top-tower air was drawn to the gas analyser through a tube with its inlet located next to the sonic anemometer. The eddy flux towers were also equipped with a range of climate sensors to measure, e.g., above canopy net radiation and photosynthetically active radiation, air temperature and humidity (Kurbatova *et al*. 2002, Tchebakova *et al*. 2002).

Calculations of half-hourly fluxes derived from the covariance between fluctuations in vertical wind-speed, and in air temperature, water vapour, and CO_2 concentration were performed online. The eddy covariance data were corrected for flux losses attributable to the incomplete spectral response of the closed-path gas analyser, to the dampening of the signal as the air moves down the suction tube, or to the separation between tube inlet and sonic anemometer head (Eugster and Senn 1995). The corrected fluxes were screened afterwards to remove poor quality data, such as typically encountered at night when wind speeds are low. This was done by identifying and excluding data at u^* (friction velocity) where NEE increased with u^* (e.g. at $u^* < 0.055$ m s^{-1} at the mire and at $u^* < 0.25$ m s^{-1} at the forest site; Arneth *et al*. 2002a, Shibistova *et al*. 2002a). Measured net exchange of carbon dioxide (NEE) was divided into its component fluxes by (i) estimating respiration from quality night-time fluxes obtained during nights above the set u^* threshold using an Arrhenius temperature dependence, and (ii) calculating photosynthesis as being the difference between NEE and respiration (for details *see* Arneth *et al*. 2002a, Lloyd *et al*. 2002a, Shibistova *et al*. 2002a). Surface conductances for water vapour exchange with the atmosphere were calculated using the Penman Monteith equation (Kelliher *et al*. 1993). Fluxes and associated climate parameters were measured more or less continuously between spring and late autumn 1998 and 2000. Due to the low temperatures and the remoteness of the sites it was difficult to maintain the measurements during winter and only in the forest were measurements continued throughout most of 1999 and 2000.

During snowmelt in spring 1999 and 2000, 10 wooden ablation poles were installed randomly in the vicinity of both eddy covariance towers. The height of snow was generally marked daily on the poles. The measurements of snowmelt began by early May 1999 and by mid April 2000. On four occasions in 1999 and 2000 snow-density in the two systems was also measured.

Results and discussion

Variations in meteorological variables and energy fluxes

Spring weather conditions in 1999 and 2000 differed significantly (Fig. 1). April 1999 was cool with a mean air temperature (T_m) of –2.9 °C, but from late April to early May temperatures increased rapidly from night-time minima of –20 °C to daytime maxima of above 20 °C. Temperatures in 2000 increased earlier — by mid April it was already quite warm ($T_m > 5$ °C) — but this was followed by an intermittent cold period before the air slowly warmed again in mid-May (Fig. 1A and B). The maximum depth of snow during winter could not be exactly quantified; at the onset of measurements it differed by ca. 15 cm between the two years (Fig. 1C and D). The overall lower snow depth in the mire in both years probably reflected the higher exposure of the mire surface to wind, with snow being transferred from the open centre to be piled along the forest-mire edges.

Snow cover provided an efficient insulation of forest and mire soils from low air temperatures. Despite mid-winter air temperatures of below –40 °C, soil and peat surface temperatures were always close to 0 °C (Arneth *et al*. 2002a, Shibistova *et al*. 2002b), and effectively decoupled from air temperatures until well after melt was complete (Fig. 1A and B). These relatively benign soil conditions despite a harsh winter

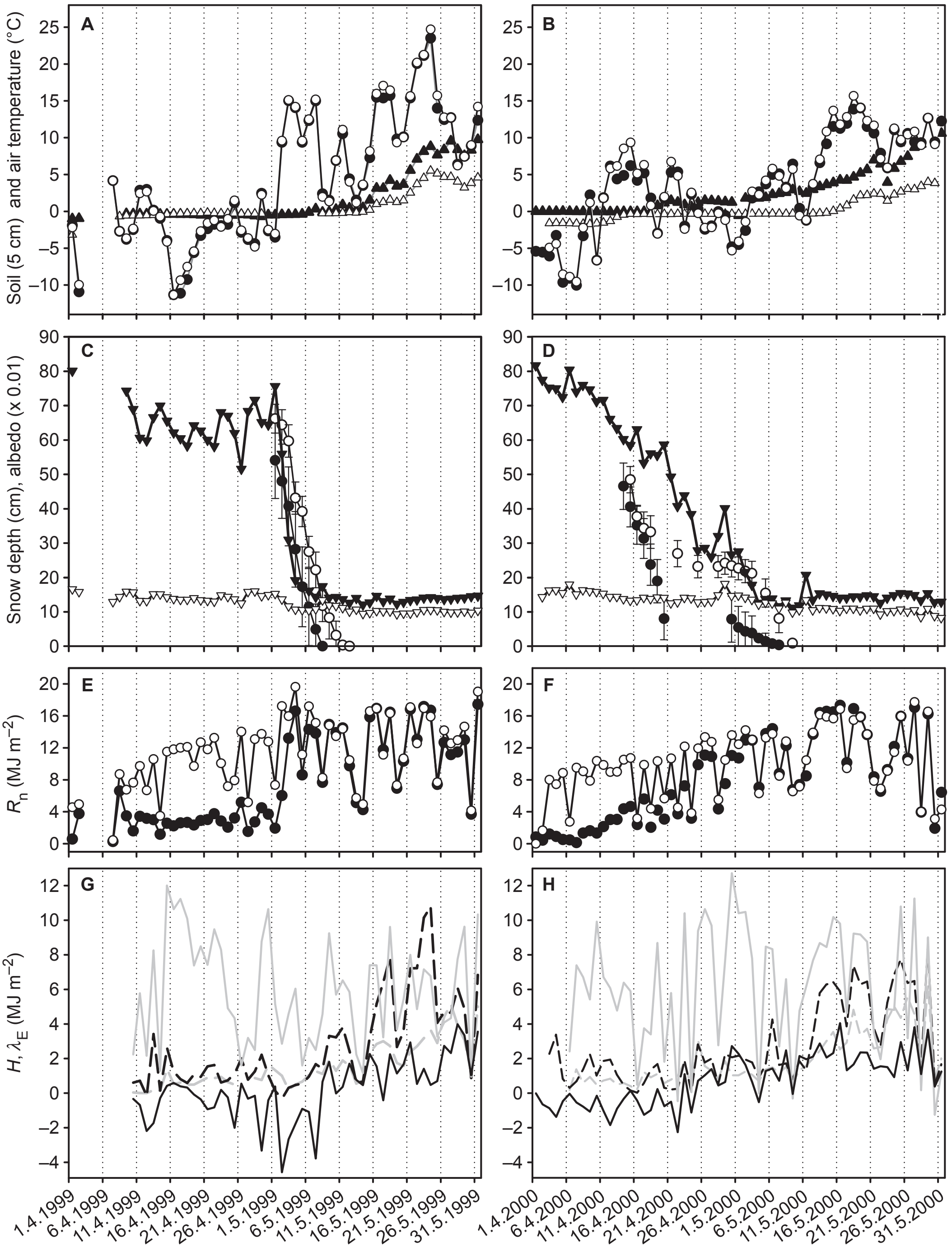

Fig. 1. Daily weather and energy fluxes in April and May at the two study sites. Panels on the left-hand side are for 1999, and those on the right-hand side for 2000. Black symbols in panels A–F denote data from the mire, white symbols from the forest. — **A** and **B**: Average daily air (circles) and soil (5-cm depth, triangles) temperatures measured at the mire and the Scots pine forest site. — **C** and **D**: Daily average short wave albedo (triangles) and snow depth (circles). Snow depth is average and standard deviation from 10 spot measurements. — **E** and **F**: Daytime net radiation sum (R_n) above the mire and the forest. — **G** and **H**: Daytime sums of sensible (H) and latent (λ_E) heat fluxes above the mire and the forest. H are denoted as grey (forest) and black (mire) solid lines, while λ_E is denoted with dashed lines using same colours.

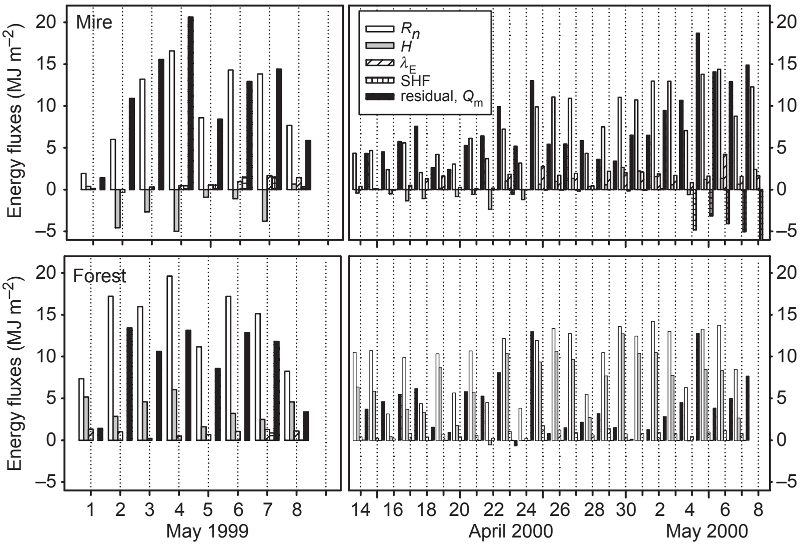

Fig. 2. Measured energy fluxes above the mire and the forest for the 1999 and 2000 snow-melt period. Abbreviations are as in Fig. 1, SHF = soil heat flux. Q_m is estimated as the residual of $(R_n - H) - \lambda_E -$ SHF.

environment lead to a continuation of microbial activity and small but measurable daily winter carbon loss which must be taken into account when deriving annual CO_2 budgets for these ecosystems (Lafleur *et al.* 1987, Fahnenstock *et al.* 1998, Arneth *et al.* 2002a, Shibistova *et al.* 2002a, Harazono *et al.* 2003, Aurela *et al.* 2004).

The different spring weather in the two study years caused the onset of snow-melt to vary by more than two weeks, it commenced on 1 May in 1999 and 15 April in 2000. The ablation rate was also quite variable. In April 2000, snow-melt effectively ceased during a 10-day period when air temperatures were close to or below zero, and snow depth remained more or less constant. Subsequently, as temperatures increased again to above 10 °C, melt was complete within a few days. In 1999, snow-melt started two weeks later than in 2000 but was much more rapid. In less than ten days of fine weather the snow pack had disappeared completely.

Melting of snow goes hand in hand with profound changes in surface radiation and energy budgets (e.g., Lafleur *et al.* 1993, Vesala 1996, Harding and Lloyd 1998, Laurila *et al.* 2001, Harazono *et al.* 2003), with the mire's shortwave reflectance (albedo) declining significantly from > 0.8 when the ground was completely snow-covered to values below 0.2 for snow-free ground (Fig. 1C and D). As the mire albedo declined, the net radiative input (R_n) into the surface increased considerably (Figs. 1E, F and 2). By contrast, the forest canopy was snow-free in spring and masked the snow underneath to a large degree, hence corresponding winter albedos were much lower with values in April already below 0.2, and dropping close to 0.1 after melt. There were only minor interannual differences in the gradually declining forest albedo despite the distinctly different melt patterns. The gradual recovery and rearrangements of photosynthetic pigments may well contribute to the steady changes in short wave reflectance (Nichol *et al.* 2002, Ensminger *et al.* 2004). The small variation in forest albedo from pre- to post-melt, and the small interannual variation illustrates the difficulties encountered when determining forest snow cover from optical remote sensing information (Grippa *et al.* 2005).

Snow-melt requires abundant energy which can be estimated based on a simplified energy balance as $Q_m = R_n - H - \lambda_E + Q_p -$ SHF, where H and λ_E are the sensible and latent heat fluxes, Q_p = energy supplied by precipitation, SHF = soil heat flux, (often negligible during melt), and Q_m is a residual energy term. This residual term subsumes processes that are difficult to measure like the rate of change in the internal snowpack energy or those occurring as ice in the snowpack or the soil underneath thaws (e.g., Prowse and Owens 1982, Cline 1997, Shook and Gray 1997, Baker *et al.* 1999). The total melt energy in the mire seemed to be only partially supplied from direct radiative sources. Negative sensible heat fluxes (H) sustained high melt rates suggesting that energy supplied to the snow pack was also drawn from surrounding air (Figs. 1G, H and 2). Melt transformed the mire's surface briefly into a shallow lake and as the water gradually warmed, drained, and evaporated the amount of energy available towards warming the air increased. Shortly after melt, the ratio of daily average evaporation (E) to its equilibrium rate (E_{eq}; Monteith and Unsworth 1990) was 0.5 but increased towards the end of May to values close to unity (not shown) but Bowen ratios remained well below unity for the entire warm season (Kurbatova *et al.* 2002). Above the forest, the energy balance was radically different from the mire in late winter/spring, with H already positive during April and with most of R_n directed towards warming the air (Figs. 1G, H and 2): there was an up to 12 MJ m^{-2} difference in above canopy R_n between the mire and the forest before melt. Only during a brief period during melt did forest H drop to values below 5 MJ m^{-2}, even on sunny days. Afterwards, a gradually increasing proportion of R_n was distributed towards λ_E but E/E_{eq} remained between 0.3 and 0.6. This suggests considerable stomatal control on transpiration from the very beginning of the warm season (cf. section *Synchronisation of photosynthesis and evapotranspiration* below) even though the soil water content was high in spring. Bowen ratios remained between ca. 1 and 4 (Tchebakova *et al.* 2002), values that are typical for boreal forests (Eugster *et al.* 2000).

Over open areas, a considerable proportion of Q_m can originate from sensible heat fluxes directed into a snow pack: on average between 0.3 and 0.6 of the total may be contributed from H (Male and Granger 1981, Prowse and Owens 1982, Kelliher *et al.* 1996, Cline 1997, Baker *et al.* 1999, Beringer *et al.* 2005). In patchy landscapes, potentially substantial advection is associated with such observations, which can be large-scale in nature (i.e., resulting from regional air mass movement) but which can also originate more localised (i.e. resulting from the discontinuous snow cover; Shook and Gray 1997). Numerical modelling studies suggest that in areas where snow-free and snow-covered vegetation exists side-by-side, and with a spatial resolution comparable to that of the forest-mire mix around Zotino, the total energy available to melt snow-covered patches can substantially increase if an abundant part of the total area is snow-free (Liston 1995). Naturally, the pine forests in the area cannot be considered as snow-free *per se*, since this is true only for the tree stems and canopy. Still, by comparing forest, shrub tundra and tundra proper, it was recently demonstrated that differences in canopy type and structure, and hence in surface albedo, snow capture and surface energy balance, had greater impact on snow-melt patterns than had large-scale latitudinal differences (J. Beringer *et al.* unpubl. data). The advective flows that may exist between the areas of contrasting surface vegetation in central Siberia await further modelling analysis (A. Sogatchev unpubl. data).

Evergreen boreal forest canopies, having low albedo, must cope with high levels of radiation in late winter/early spring, while not yet being able to open their stomata and assimilate CO_2 when air temperatures are well below zero. This poses considerable stress for the trees' photosynthetic apparatus that needs to dissipate the absorbed radiation. It is inevitable that the canopy warms considerably, hence the substantial sensible heat fluxes that were observed already in March and April — the virtually identical air temperatures that, at the same time, were observed above the forest and the mire imply efficient vertical and horizontal mixing in the near surface atmosphere (Fig. 1A and B). With respect to melt, the short wave absorption by leaves, branches and stems greatly reduces the direct radiative influx to the snow covered soil surface. Longwave radiation — a proportion of which will contribute to the energy budget at the forest's soil surface — is emitted from the above-ground parts of the trees. The amount directed towards the soil depends for instance on the canopy density and solar elevation (Sicart *et al.* 2004) and is difficult to assess without below-canopy measurements, but in some cases R_n into a forest soil surface may exceed R_n over an open area before and during melt (Male and Granger 1981, Koivusalo and Kokkonen 2002).

While not being the focal point of this analysis, the above simple energy balance calculation and the measured change in snow depth may be seen in the context of the ablation rate (M_s in mm d^{-1}), estimated as $M_s = (Q_m/(0.33 \times \varrho_s)) \times 1000$, where 0.33 is the latent heat of fusion and ϱ_s the snow pack density (510 kg m^{-3} in the mire and 390 kg m^{-3} in the forest). M_s derived from this simple calculation were between 0.7 and 1.2 of the measured rate when summed over the complete period. That such a simple calculation seems to work, increases confidence in estimates of melt over larger areas based, for instance, on satellite derived surface energy fluxes (Baker *et al.* 1999). Agreement on a day-to-day basis, however, was less good, owing mainly to the fact that additional energy inputs during rainy days are difficult to quantify, and that the density of the snowpack varied as melting progressed or rain or wet snow fell onto the snow surface.

The contrasting forest *vs.* mire surface energy balance is naturally also reflected in regional surface-atmosphere coupling. As seen above, forest H is already substantial and positive even before melt because (i) reflection of radiation is small and (ii) the available radiative energy cannot be used to evaporate/transpire water and assimilate carbon until air temperatures are above 0 °C (cf. section *CO_2 fluxes*). The canopy warms significantly above the ambient air, a process that manifests itself in near surface conditions when a dynamic convective boundary layer (CBL) can be distinguished from temperature profile measurements, which may grow up to 1.5 km above the surface as early as March for our study area (Lloyd *et al.* 2002b). By contrast, over boreal and (sub)arctic wetlands or tundra, positive sensible heat fluxes develop only after the snowpack is broken substantially. A relative shift in the proportion of forest *vs.* low mire or tundra vegetation, that has been proposed in response to climate warming, will therefore not only feed back on regional climate via changes in albedo (Foley *et al.* 1994, Betts 2000). It could also affect surface conditions via the timing of the CBL establishment and the entrainment of cool, dry free tropospheric air (Raupach 1998, Baker *et al.* 1999, Lloyd *et al.* 2002b). Across the boreal forest–tundra transition zone, the contrasts in (spring and summer) surface heating that are caused by the differences in vegetation albedo, and that convert into deep boundary layer mixing above the forest-dominated areas, have been attributed to define the position of the Arctic Front — rather than the position of the meteorological system defining the position of the tree line itself (Pielke and Vidale 1995).

CO_2 fluxes

In a manner similar to surface energy fluxes, a considerable forest-mire difference in terms of net ecosystem–atmosphere CO_2 exchange (NEE) existed in spring (Fig. 3). For the forest (and noting that, according to convention a flux from the atmosphere into the surface is negative), a relatively rapid source-sink transition of NEE from ca. 20 to 50 mmol m^{-2} d^{-1} to below –50 mmol m^{-2} d^{-1} was associated with the disappearance of snow. Fluxes reached –200 mmol m^{-2} d^{-1} already by the second half of May, about 80% of the maximum uptake observed in late July (Lloyd *et al.* 2002a). Associated with rapid spring warming in 1999, this transition to net uptake was remarkably fast: occurring over a 24 hour period (3 to 4 May). It was observed before snow-melt was complete and despite frosts below –7 °C only two nights before. When spring conditions set in more gradually (e.g. 2000) forest NEE remained above zero (i.e. a source) until but all of the snow had melted.

A considerable year-to-year variability in the timing of onset of photosynthesis is typical for northern coniferous forests, wetland and tundra. While the process is related in various ways to air temperatures it is, not surprisingly, not possible to define a single threshold that holds across the wide climatic, species and soil type range encountered in the boreal zone (Suni *et al.* 2003). For instance, the data shown in Figs. 3 (panels E and F) and 4 suggest a fast activation of readily observable forest canopy photosynthesis in 1999, but in the following year low photosynthesis rates were discernible earlier (e.g. 17 April, Fig. 4). A simple examination of the subsequent flux time series shows that in that year the canopy photosynthetic system persisted in an active yet suppressed physiological state for several days to weeks, until the onset of more persistent warm temperatures in May (Fig. 3F, inset). Assimilation rates, however, did not exceed respiration during this period.

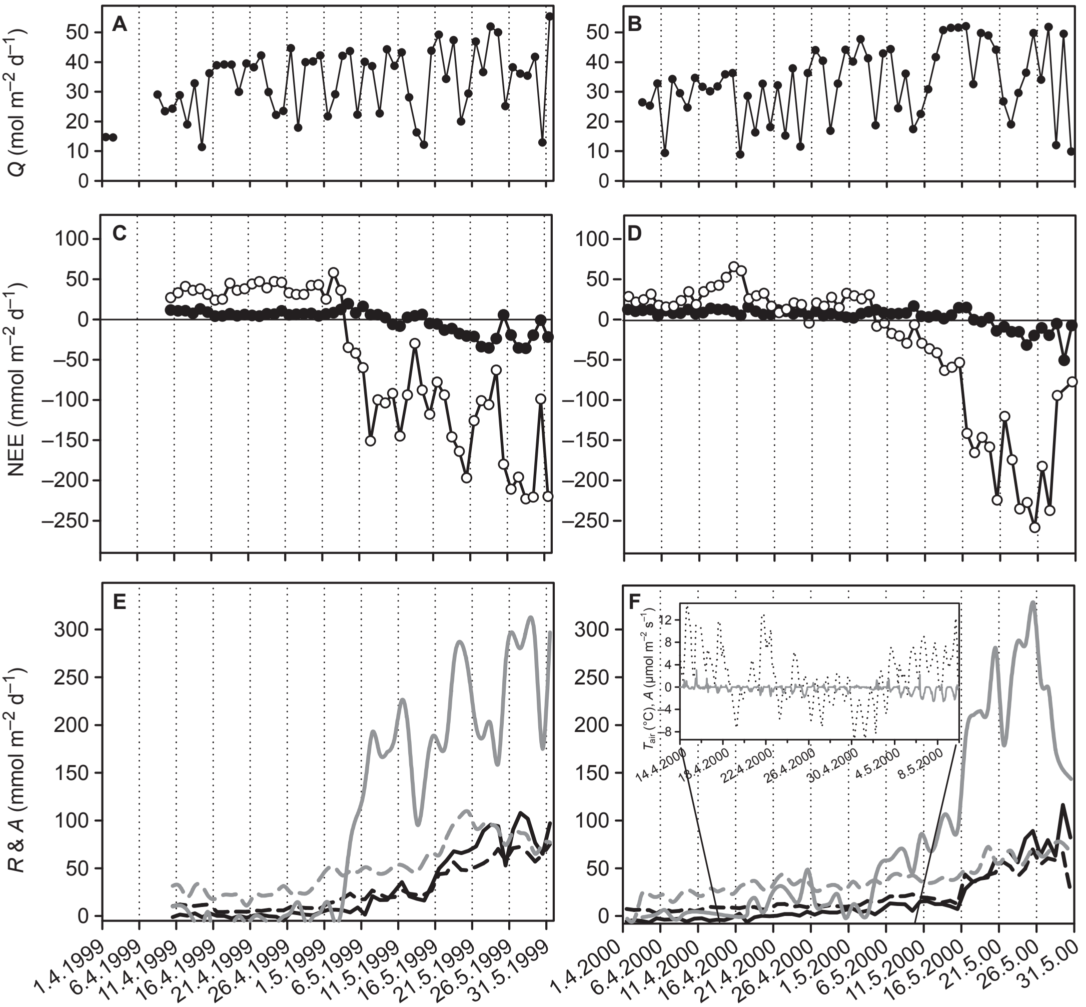

Fig. 3. Daily photonflux densities (*Q*; panels **A** and **B**), net atmosphere–ecosystem exchange of CO_2 (NEE; panels **C** and **D**: black circles = mire, open circles = forest), and respiration (*R*) (panels **E** and **F**: grey dashed line = forest, black dashed line = mire) and photosynthesis *A* (grey solid line = forest, black solid line = mire). Derivation of *R* and *A* from NEE was described in Arneth *et al.* (2002a) and Shibistova *et al.* (2002b). Photonflux densities were identical above the two ecosystems. Note that for easier comparison, assimilation and respiration data in panels **E** and **F** are both shown positive. The inset in panel **F** shows hourly air temperature (dotted line) and forest photosynthesis (solid line) between 14 April and 10 May 2000.

Above the mire, fluxes were an order of magnitude smaller as compared with those in the forest with the sink–source transition occurring between ten (1999) and fifteen (2000) days after having been observed for the forest (Fig. 3C and D). At the onset of photosynthesis, which occurred a few days before NEE became negative, rates were very low (0.5–1 μmol m^{-2} s^{-1}). In 1999 the light response curves clearly reveal triggering of photosynthesis on 7 May but for spring 2000 conditions it is unclear whether there was any photosynthetic uptake already before 14 May (Figs. 3 and 4).

The photosynthetic light response curves for mire and forest for selected periods shown in Fig. 4 demonstrate how the increase in daily photosynthesis (*A*) during post-melt (Fig. 3) results from concomitant increases in maximum rates and quantum use efficiencies, both of which could change significantly even between individual days (cf., for instance 3 *vs.* 4 *vs.* 5 and 6 May in the forest in 1999, or 6 *vs.* 7 May in

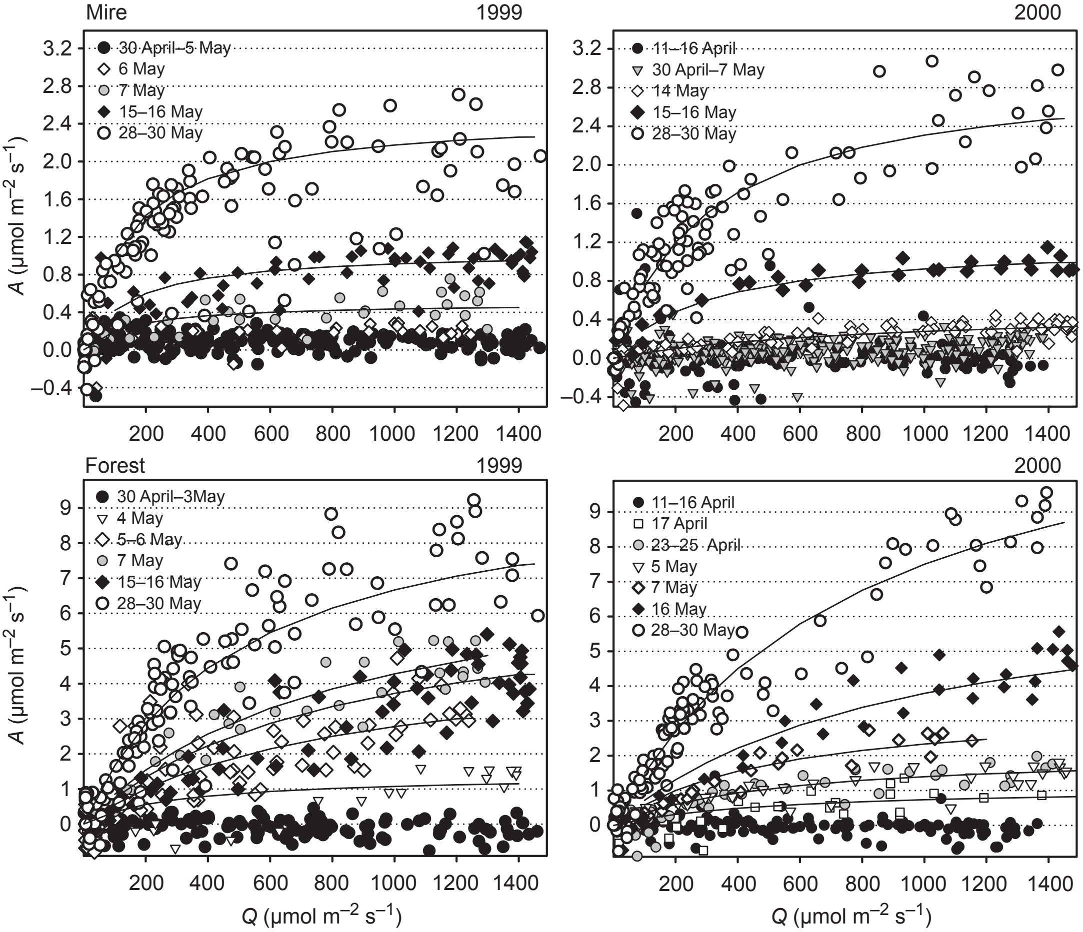

Fig. 4. Example ecosystem photosynthesis light responses during selected spring periods 1999 and 2000 in the mire and in the forest. The lines are hyperbolical fits through the data, drawn to guide the eye, and follow $A = a \times Q/(b + Q)$.

the mire). In the boreal evergreen environment photosynthesis in spring requires, amongst other things, positive air temperatures and availability of liquid soil water to be conducted to the green tissues. Immediately after the first day of snow-melt, soil temperatures underneath the snow cover rise to 0 °C (Fig. 1A and B; Shibistova *et al*. 2002b), remaining so until the completion of snow-melt — the so called zero-curtain effect where liquid water is present in equilibrium with melting ice (Lloyd *et al*. 2002a). Presumably, as long as this condition is met, favourable air temperatures should allow photosynthesis to commence, irrespective of snow cover (Pelkonen and Hari 1980, Bergh and Linder 1999). Thus, in 2000, when air temperatures increased slowly and in an intermittent fashion, low rates of carbon uptake were observed for an extended period while the ground was still covered by snow.

Winter temperatures in the Zotino area may fall below –50 °C and even by mid-April night-time frosts are still frequently below –15 °C during which time the protein of the PS II reaction centre would have been at least inactive, if not lost completely (Ensminger *et al*. 2004). Bearing in mind already substantial levels of solar radiation in northern latitudes after the vernal equinox (quantum flux maxima around 1400 μmol m^{-2} s^{-1} by mid April, Fig. 4) needle pigment composition in spring must foster the dissipation of absorbed radiative energy to avoid

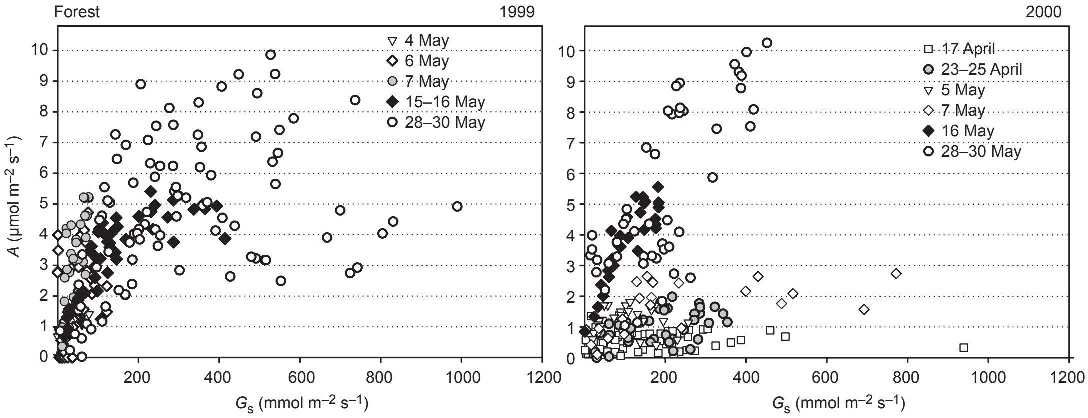

Fig. 5. Relationship between the forest's net photosynthesis (A) and surface conductance (G_s) during selected spring periods 1999 and 2000. G_s were calculated using the Penman Monteith equation.

damage while the reductive pentose phosphate pathway is suppressed. Accordingly the needle xantophyll cycle pool in April is high (Demming-Adams and Adams 1996, Nichol *et al.* 2002, Ensminger *et al.* 2004), decreasing progressively until June and accompanying the rapidly accelerating canopy photosynthesis. The normalised de-epoxidation (DEPS) status of the xantophyll cycle pigments, a measure for the activeness of xantophyll cycle pigments, thus decreases as canopy photosynthesis increases, which leads to a linear relationship even for whole forest NEE with DEPS (Ensminger *et al.* 2004). We are not aware of investigations of spring pigment composition in wetland species. But the visual inspection of, for instance, much of the *Sphagnum* ssp. at Zotino that was covered by snow during winter, turning from brownish red to bright green rapidly within only some weeks after melt, support the notion that here too a significant and rapid change in pigment content accompanied the general recovery after winter. The mire's NDVI was much lower than the forest in early May but increased continuously until a plateau was reached by around mid-June (Nichol *et al.* 2002).

Synchronisation of photosynthesis and evapotranspiration

For a few days immediately preceding melt, while rates of photosynthesis were still zero, forest G_s could reach values > 1000 mmol m^{-2} s^{-1}, reflecting some evaporation while air saturation deficit was very low (< 0.3 kPa), and contrasting the much lower values in the mire (250 mmol m^{-2} s^{-1}; not shown). As soon as A became discernible this relationship changed drastically in the forest; by then A increased very steeply with G_s (Fig. 5) and the relationship displayed the typical saturation of A with G_s, in this case at G_s around 200 mmol m^{-2} s^{-1}. Simultaneously, A and λ_E increased nearly linearly up to A ca. 9 μmol m^{-2} s^{-1} (Fig. 6). Post-melt diurnal and daily variation in G_s are dominated by variations in canopy conductance (G_c) based on a strong linear relationship between G_s and G_c that was established using a below canopy eddy flux measurement system that was in place during melt 2000 (not shown). In 2000, from mid-May onwards, photosynthetic rates at a given canopy and surface conductance were somewhat larger when compared with those in 1999 (Fig. 5), and continued to remain so throughout the active period (Lloyd *et al.* 2002a). One might suggest a lasting effect of the early active-season weather patterns since the somewhat longer and more gradual onset of spring in 2000 would have led to needle pigment recovery being slightly more advanced by the end of May when compared with that in the previous year. An alternative explanation was discussed by Lloyd *et al.* (2002a) who found reduced stem growth in the pine forest in 1999 (as compared with that in 1998 and 2000) which may have fostered alloca-

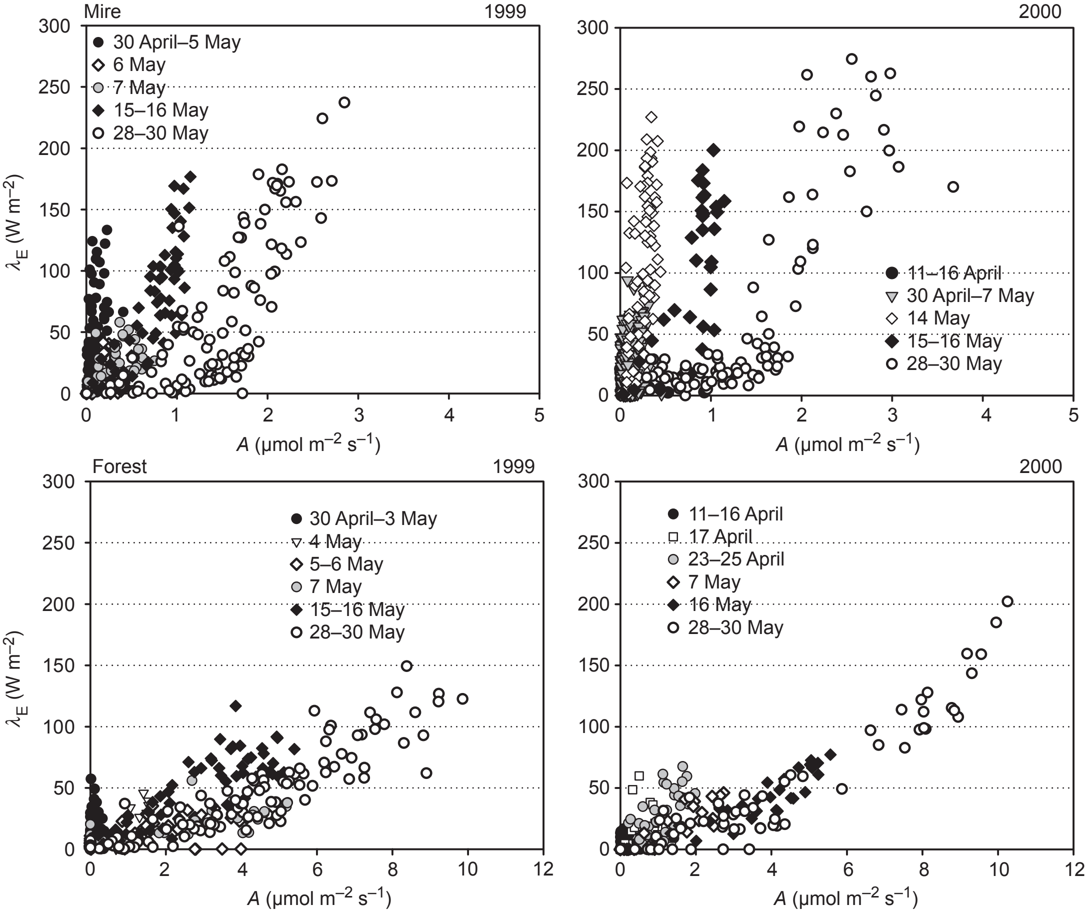

Fig. 6. Relationship between ecosystem net photosynthesis (A) and latent heat flux (λ_E) during selected spring periods in 1999 and 2000 in the mire and in the forest.

tion of carbon to fine root growth — enhancing tree water and nutrient uptake. In both years, forest G_s rarely exceeded 500 mmol m^{-2} s^{-1} once stomata had opened. Low maximum canopy and surface conductances are to be expected, reflecting the area's nutrient-poor, sandy soils with a low water storage capacity (Schulze *et al.* 1995, Kelliher *et al.* 1997, Lloyd *et al.* 2002a).

We observed the pine needle stomata at the study site being sealed with a wax-like "plug" towards the end of winter. Visible as dark inclusions in the stomatal cavity in needles collected in late February, these were absent during summer (Fig. 7). These plugs possibly help to avoid frost desiccation during the cold Siberian winter and were observed in Russia already in the 1960s (Khlebnikova *et al.* 1963). They are — to the best of our knowledge — absent in Scots pine growing in the somewhat more balmy environment of northern Europe. Degradation of this "plug" must occur in early spring, allowing the diffusion of CO_2 into the leaves, which naturally must go hand in hand with considerable changes in surface and canopy conductances as latent heat fluxes were dominated by transpiration after melt. We do not have a time series of needle photographs available from the area and the question whether the "plug" degraded prior to, or simultaneously with, onset of photosynthesis warrants further investigation.

In the mire a much larger proportion of surface exchange processes is expected to occur without stomatal control, since a significant proportion of the area was covered by non-vascular species, pools of free water, or water saturated surfaces. Maximum surface evapotranspiration

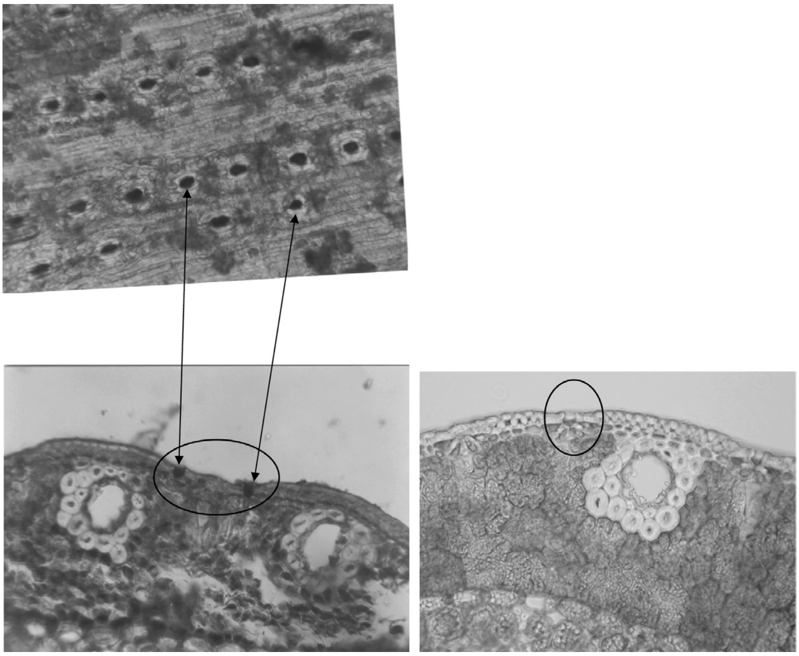

Fig. 7. Photographs of Scots pine needle sections before snow-melt (left) and from summer (right). Stomata are encircled in the cross-sectional photographs. Dark stains in the stomata from late-winter needles show the presence of dark, wax-like plugs that may help to prevent frost desiccation and that are absent from summer needles (example from June 2005). The pre-melt needles were collected in late February 2000 and transported at sub-zero temperatures. Needles were stored in acetate prior to taking the photographs.

exceeded that of forest by ca. 50–100 W m^{-2} (Fig. 6) and high values of G_s after melt, exceeding 500 mmol m^{-2} s^{-1} (Kurbatova *et al.* 2002), reflect the significant areas of open water which fill the peat hollows. λ_E and A varied largely independently from each other as evapotranspiration continued to increase even when A was constrained by cellular biochemistry. The threshold for the saturation in the relationship between the two increased rapidly after melt (Fig. 6), with distinct shifts from one day to the next.

Spring fluxes in relation to the snow-free and annual carbon and water budgets

As is shown above, at the two study sites in central Siberia the timing and speed of snowmelt and the rates of the associated reactivation of ecosystem physiological activity were remarkably different between the two study years. Such variability seems typical for the boreal and arctic zones (Lafleur *et al.* 1987, Harazono *et al.* 2003, Suni *et al.* 2003, Aurela *et al.* 2004). But does such behaviour necessarily affect annual ecosystem carbon balances significantly? With only two years of data this question naturally cannot be answered with any statistical certainty for the two central Siberian sites. Nevertheless, since the connection between timing of spring melt, length of active season and annual carbon and water balance differs between ecosystems and regions it may be useful here to briefly discuss our observations in view of the entire snow-free season, and to view them in context with observations at a range of other field sites.

Using the term “spring” as coinciding with the months of April and May it is clear that carbon and water balances of the forest versus those of the mire responded to year-to-tear variation in spring in a different way. Especially so in May, when carbon fluxes in the forest were almost identical for both years, but vastly different for the mire (Table 1). For these same two years, the annual carbon balance of the forest — examined in some detail by Lloyd *et al.* (2002a)

Table 1. Monthly sums of spring ecosystem CO_2 uptake (NEE) and evapotranspiration (E).

	Mire NEE (mmol m^{-2})	Mire E (mm)	Forest NEE (mmol m^{-2})	Forest E (mm)
April 1999	0.15	10	0.9	6
May 1999	–0.23	47	–3.3	26
April 2000	0.29	14	0.8	8
May 2000	–0.05	50	–3.2	26

and Shibistova *et al*. (2002a) — was estimated to be identical at –13 mol m^{-2} but differed by nearly a factor of two in the mire (–1.8 mol m^{-2} in 1999, and –3.0 mol m^{-2} in 2000; Arneth *et al*. 2002a). At a glance, this seems to indicate a negative influence of timing of the onset of snowmelt on NEE in the mire while there was none on the forest's NEE.

Based on six years of eddy flux data, Aurela *et al*. (2004) put forward statistical arguments for the annual CO$_2$ budget of their Finnish mire site being correlated with the river discharge and mire water table depth which in turn depend on the timing of spring flood. Annual precipitation and total evaporation are quite similar in the Finnish and Siberian sites (470 and 260 mm, respectively, in Finland, and 530 and 290 mm in Siberia). In both the Finnish and Siberian mires seasonal NEE peaked in June and July, with considerable inter annual variation being possible at the Finnish site in June and in Siberia in July (Arneth *et al*. 2002a, Aurela *et al*. 2004).

In the case of our pine forest interannual variation of NEE was small; any climate factors that stimulated photosynthesis quite obviously had similar effects on respiration at least when integrated over the season. The photosynthetic pigment content of the needles is high enough for spring photosynthesis to contribute notably to the annual NEE totals although a too early recovery of pigments in Scots pine needles can be counteracted by repair costs and increased maintenance respiration from subsequent frost or cold periods (Ensminger *et al*. 2004). A brief synthesis across a range of mires, evergreen and deciduous coniferous ecosystems in Siberia and European Russia (Arneth *et al*. 2002a, Knohl *et al*. 2002, Lloyd *et al*. 2002a, Milyukova *et al*. 2002, Röser *et al*. 2002) revealed that at these sites summer (July) NEE dominates NEE over the snow-free season, with typically 30% to 50% of the snowfree net carbon uptake (or loss) taking place in that single month (A. Arneth unpubl. data). If an advanced spring-recovery were to result in these ecosystems reaching their maximum uptake capacity earlier the thus prolonged period of peak NEE could indeed lead to higher annual net uptake. But likewise, a proportionally very small reduction in carbon fluxes during these peak times in summer that are not related to spring conditions (for instance dry summer weather) may well have a greater effect on ecosystem carbon balances than proportionally larger changes in spring when fluxes are, in any case, low.

Summary and conclusion

Few studies to date have investigated in detail the concomitant changes in northern ecosystem radiation and energy balance, and surface–atmosphere exchange of CO$_2$ encountered during spring snow-melt. The period of spring recovery is critical in the northern high latitudes, since its timing and speed can have a bearing on environmental conditions and surface–atmosphere exchange during the rest of the year. However, particularly in heterogeneous landscapes with sharply contrasting surface vegetation cover, field observations that could be used for testing or accurate parameterisation of models that seek to predict these effects are required.

Large differences in forest *vs*. mire albedo before and during melt resulted in strongly dissimilar above-canopy net-radiation, sensible and latent heat fluxes. R_n above the forest was generally two to three times higher as compared with that above the mire, and the dominant proportion was partitioned into sensible heat flux directed towards the atmosphere. In the mire, the radiative energy required to melt the snow was on some days amplified considerably by negative sensible heat fluxes. If such contrasts in surface energy partitioning over heterogeneous landscapes are not captured in catchment, regional or larger scale models, the establishment and height of the convective boundary layer, and hence surface–troposphere exchange and mixing will be misrepresented. This has important consequences for analyses of surface emissions (e.g., the computation of trace gas concentrations based on surface processes) as well as surface climate (e.g., via effects of entrainment).

Time is something which is not abundant in the continental boreal environment where only during three to four months of the year climatic conditions allow for production and regeneration. As a consequence, the photosynthetic machinery is well adapted to an immediate response to above zero temperatures and spring snow-melt, manifested in the impressively speedy recovery of physiological activity. Photosynthesis rates — at a given light — could double from one day to the next during the very early stages of recovery, both in the forest and in the mire. Low rates of forest carbon assimilation were possible even before melt was complete (and NEE became negative), re-emphasizing that air temperatures are a major controlling factor in these environments. As liquid water became available for evapotranspiration, latent heat fluxes increased steadily at both sites, with forest A and λ_E being tightly linked and a typical curvlilinear relationship between A and G_s emerging. Above the mire, λ_E and A varied more or less independently from each other which is to be expected for an ecosystem where neither of the two is influenced to a large degree by stomatal control during the early active season.

Vegetation type and structure affect processes during spring and these may propagate to summer conditions thus influencing C uptake and energy partitioning for an entire year. However, it is important to recognise that it may not be the actual timing of spring *per se* that may impact the carbon and water balance, but a combination of the onset *and* speed of melt *and* climate conditions during the rest of the year. As so often, simple climate responses in the natural environment may not hold when a range of systems is being considered.

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