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Seasonal and annual variations in the photosynthetic productivity and carbon balance of a central Siberian pine forest

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ABSTRACT

We present a first analysis of data (June 1998 to December 2000) from the long-term eddy covariance site established in a *Pinus sylvestris* stand near Zotino in central Siberia as part of the EUROSIBERIAN CARBONFLUX project. As well as examining seasonal patterns in net ecosystem exchange (N_E), daily, seasonal and annual estimates of the canopy photosynthesis (or gross primary productivity, G_P) were obtained using N_E and ecosystem respiration measurements.

Although the forest was a small (but significant) source of CO_2 throughout the snow season (typically mid-October to early May) there was a rapid commencement of photosynthetic capacity shortly following the commencement of above-zero air temperatures in spring: in 1999 the forest went from a quiescent state to significant photosynthetic activity in only a few days. Nevertheless, canopy photosynthetic capacity was observed to continue to increase slowly throughout the summer months for both 1999 and 2000, reaching a maximum capacity in early August. During September there was a marked decline in canopy photosynthesis which was only partially attributable to less favourable environmental conditions. This suggests a reduction in canopy photosynthetic capacity in autumn, perhaps associated with the cold hardening process. For individual time periods the canopy photosynthetic rate was mostly dependent upon incoming photon irradiance. However, reductions in both canopy conductance and overall photosynthetic rate in response to high canopy-to-air vapour differences were clearly evident on hot dry days. The relationship between canopy conductance and photosynthesis was examined using Cowan's notion of optimality in which stomata serve to maximise the marginal evaporative cost of plant carbon gain. The associated Lagrangian multiplier (λ) was surprisingly constant throughout the growing season. Somewhat remarkably, however, its value was markedly different between years, being 416 mol mol^{-1} in 1999 but 815 mol mol^{-1} in 2000. Overall the forest was a substantial sink for CO_2 in both 1999 and 2000: around 13 mol C m^{-2} a^{-1}. Data from this experiment, when combined with estimates of net primary productivity from biomass sampling suggest that about 20% of this sink was associated with increasing plant biomass and about 80% with an increase in the litter and soil organic carbon pools. This high implied rate of carbon accumulation in the litter soil organic matter pool seems unsustainable in the long term and is hard to explain on the basis of current knowledge.

1. Introduction

The rate of increase in atmospheric carbon dioxide concentrations is less than expected on the basis of emissions from fossil-fuel burning and land-use change. Not all of this "missing" CO_2 can be accounted for by oceanic uptake (Orr et al., 2001), implying a substantial terrestrial sink, most likely located in both the northern latitudes and in the tropics (Prentice et al., 2001). Various hypotheses and calculations have been presented arguing that, depending on

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location, this sink might be a consequence of long-term increases in CO_2 concentration and increased rates of nitrogen deposition, as well as changes in land-use patterns or climate change itself (Lloyd, 1999a; Prentice et al., 2001).

Although many atmospheric inversion studies have suggested a substantial northern hemisphere terrestrial sink for CO_2 (Tans et al., 1990; Fan et al., 1998; Rayner et al., 1999; Kaminski et al., 1999; Ciais et al., 2000) there is still great uncertainty as to how this supposed sink is distributed. Fan et al. (1999) claimed that the conterminous USA constituted by far the most substantial component, but the inversion study of Kaminski et al. (1999) attributed about 70% of the northern hemisphere terrestrial sink in the early 1980s to the former USSR. Ciais et al. (2000) also found that Siberia constituted the dominant component of their estimated northern hemisphere sink. On the other hand, Rayner et al. (1999) concluded a much smaller northern sink than other atmospheric inversion studies, with the Siberian landmass being more or less carbon neutral.

Schulze et al. (1999) suggested that despite their large area the low average productivity of Siberian forests mitigates against a significant component of the terrestrial sink for anthropogenic CO_2 being located in the Siberian boreal zone. This is supported by theoretical considerations. For example, Lloyd and Farquhar (1996) argued that only moderate temperatures during summer should limit the responsiveness of boreal photosynthesis to increasing atmospheric CO_2 concentrations. However, they also suggested that the growth response to any stimulation of photosynthesis by increasing CO_2 concentrations should be greatest in plants which consume a high proportion of their annual photosynthetic carbon acquisition (gross primary productivity, G_P) in autotrophic respiration rather than growth. Interestingly, recent work in boreal forests has indicated that the fraction of G_P consumed as autotrophic respiration (φ) is higher than was previously considered the case and probably greater than φ for temperate forest ecosystems (Baldocchi et al., 1997; Ryan et al., 1997; see also this study). This suggests that the growth response of boreal forests to increasing atmospheric CO_2 concentrations might be greater than previously thought, even when potential nitrogen constraints on this response are taken into account (Lloyd, 1999b).

Long-term *in situ* measurements of ecosystem carbon fluxes by the eddy covariance technique provide one technique for assessing an ecosystem's carbon balance (Baldocchi et al., 1996). Although it is clear that the specific site history must exert a large effect of the measured carbon balance of any particular stand (Schulze et al., 1999), particularly in respect of respiratory fluxes (Sawamoto et al., 2000; Janssens et al., 2001), when results from several eddy covariance measurement stands are synthesized together, specific and informative patterns may emerge (Baldocchi et al., 2001). Likewise, the examination of respiratory and photosynthetic carbon fluxes for the one site but over several years may allow useful information on the sensitivity of these fluxes to climate to be evaluated (Goulden et al., 1996; Goulden et al., 1998; Lindroth et al., 1998; Milyukova et al., 2002). Useful information may also even be obtained in the absence of any experimental or network "design". For example, the three long-term studies of mature boreal coniferous forest carbon balance reported to date, viz. Lindroth et al. (1998) in Sweden, Goulden et al. (1998) in Canada and Milyukova et al. (2002) in European Russia all observe their forests to be substantial sources of CO_2 to the atmosphere; especially in warmer years.

The current paper is the third in a series examining carbon fluxes for a 200-year-old *Pinus sylvestris* L. stand growing near Zotino in central Siberia. Other papers deal with respiratory processes in some detail (Shibistova et al., 2002a, 2002b), and we focus here on the photosynthetic productivity of the forest and its environmental regulation. We also employ our estimates of annual gross primary productivity (photosynthesis) in conjunction with soil, stem and leaf respiration measurements (Shibistova et al., 2002b), as well as independent biomass-based estimates of net primary productivity (Wirth et al., 2002a), to quantify the various flows of carbon within this boreal ecosystem. We conclude that, in contrast to most other mature boreal forests studied to date, the Zotino forest is a strong sink for CO_2, with most of this sequestered carbon accumulating in the soil organic carbon pool.

2. Materials and methods

2.1. Site description

The experimental site was located about 30 km west of the Yenisei river (60°45′ N, 89°23′ E, elevation 90 m a.s.l.), located on the eastern edge of the West Siberian Plain. The landscape of this region is represented by mosaic structure, including forests occurring on alluvial sand dunes surrounded by sphagnum peat bogs and river meanders (Lloyd et al., 2001).

The fire successional pine (*Pinus sylvestris* L.) forest chosen for eddy covariance measurements was about 200 years old and a homogeneous stand characterised by an open canopy and a leaf area index (LAI) of about 1.5 (projected basis). The stem density within the forest has been estimated at around 450 ha^{-1}, basal area at 30 m^{-2} ha^{-1} and biomass (dry weight) of about 10.7 kg m^{-2} (Wirth et al., 1999). In that paper the stand is designated as 200_{ld}. Additional information is also available in Wirth et al. (2002a,b,c) and Table 1 of this paper. The above-ground vegetation was dominated by lichens (C*ladina* spp., C*ladonia* spp.) and intermittent dwarf erichoid shrubs (V*accinium* spp.). The stand was located on gently undulating, alluvial sands (classified as Inceptisols) with no underlying permafrost. The sandy mineral soil has been described in detail by Bird et al. (2002) and Šantrůčková et al. (2002).

2.2. *Determination of ecosystem fluxes of CO_2, water vapour and energy*

Eddy covariance measurements of carbon dioxide, water vapour, heat and momentum fluxes were made at a height of 25.2 m, about 5 m above the average tree height and 2 m above the highest nearby trees. The measurement system consisted of a triaxial sonic anemometer (model Solent R3, Gill Instruments, Lymington, UK) and a fast response CO_2/H_2O non-dispersive infrared gas analyser (model 6262-3, LiCor Inc., Lincoln, NB, USA). The air was drawn from an inlet at the top of the tower, 20 cm below the sonic measurement height, through BEV-A-Line tubing (33 m length and 5 mm inner diameter) and two aerosol filters (ACRO 50 PTFE 1 μm pore-size, Gelman, Ann Arbor, MI, USA) at a flow rate of 4–5 L min^{-1} (pump unit: KNF Neuberger, Germany). Output from the sonic anemometer and infrared gas analyser was read at 20 Hz through RS-232 ports onto 386-class computers, and all data was stored for subsequent analysis. The pressure in the IRGA cell, as measured by the internal pressure sensor, was about 10 mbar above ambient.

Ambient CO_2 concentrations at heights of 0.1, 1.0, 2.0, 4.8, 8.0, 16.0, 24.0 and 25.2 m were also recorded with a system consisting of a LiCor nondispersive infrared gas analyser (model 6251, LiCor Inc., Lincoln, NB, USA), pump (KNF, Neuberger, Germany), switching manifold, BEV-A-Line tubing and datalogger (Campbell, model CR23X). Air was drawn through the tubes at a rate of 7 L min^{-1}, with each height being sampled for 2 min, with readings taken at a rate of 1 Hz over the last 10 s of sampling at each height and averaged before being stored.

The fluxes were calculated offline using covariances of 60 min high-frequency time series of vertical wind velocity and temperature, CO_2 density and water vapour density. For the eddy covariance system installed above the canopy, the time lag between measurements of vertical wind velocity and scalar densities arising from transport down the tube was estimated by cross-correlation between both time series and found to be equal to approximately 5.5 s for carbon dioxide and 6.0 s for water vapour. The data were corrected by shifting the time series by the estimated time lag.

Frequency losses due to damping in the tube and analyser response were corrected for using the approach of Eugster and Senn (1995). The correction parameter ("inductance") was determined from the cospectral analysis of vertical wind, temperature, carbon dioxide and water vapour time series. For CO_2, the main subject of this paper, values were typically in the range 0.15–0.20. Water vapour dilution corrections were made with internal software of the LiCor 6262 instrument, and corrections of differences of the air pressure in the sampling cell and in the atmosphere were calculated automatically with the built-in pressure transducer. Coordinate rotation as in McMillen (1988) was applied.

The net rate of carbon exchange by the ecosystem (N_{E}) was then determined as one-dimensional mass balance as

$$N_{\text{E}} = F_h + \int_0^h \frac{\partial C_{\text{a}}}{\partial t}\,\text{d}z, \tag{1}$$

where F_h is the flux of CO_2 at some height h above the canopy top as measured by eddy covariance, C_{a} represents the measured CO_2 concentration(s) at height z above the soil and t is time.

Measurements presented here cover the period from early June 1998 to the end of December 2000. The eddy covariance equipment was decommissioned for the first winter season (October 1998 through March 1999) but, apart from the period 21 December 1999 to 20 January 2000 where measurements were not possible due to instrumental failure, the eddy covariance system remained operational throughout the winter of 1999/2000. Because of power supply constraints in winter, the CO_2 profiling system was only operative for the period May through October for both 1999 and 2000.

2.3. *Supplementary meteorological measurements*

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

Five soil heat flux plates (model Rimco HFP-CN3, McVan Instruments, Melbourne Australia) installed at a depth of 4–5 cm, were used to get an average soil heat flux in the vicinity of the tower. Soil temperature was measured by PT 100 sensors at two profiles at depths of 5, 15, 50 and 100 cm and then averaged for each depth. All meteorological data were collected every 10 s, and 10 min averages or sums (precipitation only) were stored on a datalogger (Dl 3000, DeltaT, Burwell, UK).

2.4. *Calculation of canopy net assimilation rate*

From May through September 1999 and April through mid-October 2000 a second eddy covariance system was employed beneath the forest canopy at a height of 2.5 m above the forest floor. This system, described in detail in Shibistova et al. (2002a) was identical to that installed for above-canopy measurements (Section 2.2), but with the air drawn 10 cm below the sonic measurement height at a flow rate of 5.8 L min^{-1}.

Data were processed as described above with the time lag due to transport in the tube estimated at 1.5 s for carbon dioxide. The inductance was determined on weekly blocks of data and was typically 0.25.

The net rate of carbon assimilation by the canopy foliage, A_{C}, was then estimated as

$$A_{\mathrm{C}} = F_g - F_h - \int_g^h \frac{\partial C_{\mathrm{a}}}{\partial t}\,\mathrm{d}z + 0.85 R_{\mathrm{st}}, \qquad (2)$$

where F_g is the net flux of CO_2 as measured at 2.5 m height. The integrand in eq. (2) was determined from CO_2 measurements made at the 2.0, 4.8, 8.0, 16.0, 24.0 and 25.2 m levels, with the value at g (2.5 m) inferred by interpolation. The final term in eq. (2) is relatively small (typically less than 1.0 μmol m^{-2} s^{-1}), but allows for respiration by the stem volume above 2.5 m height. Hourly estimates of R_{st} have been taken from the study of Shibistova et al. (2002b).

As with our night-time foliage respiration estimates in Shibistova et al. (2002b), we applied stringent data quality criteria. Following the approach of Foken and Wichura (1996) we applied "stationarity tests", only accepting estimates of A_{C} if the flux dispersion was less than 0.5 for both F_g and F_h.

2.5. *Estimation of gross primary productivity*

As is discussed elsewhere (Shibistova et al., 2002b), gross primary productivity (G_{P}) used in this study is defined as

$$G_{\mathrm{P}} = \max[A_{\mathrm{C}}, 0]. \qquad (3)$$

This formulation allows for negative carbon gain by the foliage in the light to be included in the ecosystem respiratory budget. This is an important feature of our ecosystem in spring. It also eliminates the need to estimate the unknown contribution of non-photorespiratory mitochondial CO_2 release in the light (Shibistova et al., 2002b).

2.6. *Calculation of canopy evaporation rate*

As for canopy photosynthesis (Section 2.4) the evaporation rate from canopy foliage, E_{C}, was estimated as the difference between the two eddy covariance systems, viz.

$$E_{\mathrm{C}} = E_h - E_g, \qquad (4)$$

where E_h is the evaporation rate measured above the canopy and E_g is the evaporation rate measured above the forest floor. Equation (4) ignores any changes in water vapor content within the canopy itself, as well as any possible evaporation from stems and branches.

2.7. *Calculation of canopy conductance to water vapour transfer*

The canopy conductance to water vapor transfer, G_{C}, was calculated from inversion of the Penman–Monteith equation, modified to allow for latent and sensible heat fluxes from the soil. The equation used was

$$r_c = \frac{sr_a(R_n - \Lambda E_h - H_g) + \rho_a C_p D}{\gamma \Lambda E_C} - r_a, \quad (5a)$$

where r_c (s m^{-1}) is the associated canopy resistance to water vapour transfer ($= 1/G_C$), r_a is the aerodynamic resistance (s m^{-1}), s is the rate of change in the saturation vapour pressure of water with temperature (Pa K^{-1}), R_n is the net radiation as measured above the canopy (W m^{-2}), λE_h is the latent heat flux measured above the canopy (W m^{-2}), H_g is the sensible heat flux measured above the forest floor (W m^{-2}), ρ_a is the density of air (kg m^{-3}), C_p is the heat capacity of air (J kg^{-1} K^{-1}), D is the vapour pressure deficit (Pa), γ is the psycrometric constant (Pa) and ΛE_C is the canopy latent heat flux (W m^{-2}).

In order to estimate r_a and its dependence on the prevailing meteorological conditions, we used the following equations (Lloyd et al., 1995)

$$r_a = \frac{u}{u_*^2} + \frac{1.5 + \psi_m - \psi_h}{k u_*}, \quad (5b)$$

where u is the mean vertical windspeed as measured by the sonic anemometer above the tower, u_* is the friction velocity as calculated from the covariance of the measured vertical and horizontal velocity fluctuations, ψ_m and ψ_h are the dimensionless integrated abiatic profile correction factors for momentum and heat flux, respectively (Paulson, 1970; Garratt, 1992), and k is von Karmen's constant, taken here as 0.41. The factor 1.5 allows for the different surface roughness length for heat, water vapour and CO_2 as opposed to that for momentum (Garratt, 1992).

In order to calculate ψ_m and ψ_h we used the following under unstable and near-neutral conditions ($L < 0$)

$$\psi_m = \ln\left(\frac{(1+x^2)(1+x)^2}{8}\right) - \mathrm{a}\tan(x) + \pi, \quad (6a)$$

and

$$\psi_h = 2\ln\left(\frac{1+x^2}{2}\right), \quad (6b)$$

where x is defined as

$$x = \left(1 - \frac{15(Z-d)}{L}\right)^{0.25}, \quad (6c)$$

with Z being the measurement height (25.2 m) and d being the zero plane displacement height, taken here as $0.7h_C = 15.4$ m where h_C is the canopy height, taken here as 20 m. In eq. (6c) L is the Monin-Obukov length, calculated according to

$$L = \frac{-u^{*3}\rho_a T_a C_p}{k g H_h}, \quad (6d)$$

where T_a is the air temperature in K, g is the acceleration due to gravity (9.81 m s^{-2}) and H_h is the sensible heat flux above the canopy (W m^{-2}). Within eq. (6c) the term $(Z-d)/L$ was constrained to have a minimum value of -5 for numerical reasons.

For stable conditions $(L > 0)(Z-d)/L$ was also constrained, in this case to be always less than or equal to 1.0 with

$$\psi_m = \psi_h = \frac{-5(Z-d)}{L}, \quad (6e)$$

(Garratt, 1992).

Canopy conductances (m s^{-1}) as derived from eq. (5) in conjunction with equations (6) were then converted to molar units (Cowan, 1977) by multiplying them by $P/(RT_C)$, where P is the atmospheric pressure as measured above the canopy, R is the universal gas constant and T_C is the canopy temperature in K, calculated as

$$T_C = T_a + \frac{r_a H_h}{C_p \rho_a}. \quad (7)$$

Likewise the water vapour content of the canopy air, e_C, was calculated as

$$e_C = e_a + \frac{r_a E_h}{\rho_a}. \quad (8)$$

where e_a is the the water vapour content of the air as measured at the top of the tower. This allowed the canopy-to-air vapour pressure difference, D_C, to be calculated as the difference between e_c and the saturation vapour pressure of water at T_C.

3. Results

3.1. Seasonal variations in canopy CO_2 assimilation characteristics

Figure 1 illustrates average diurnal variations in incoming photosynthetically active radiation (I), canopy CO_2 assimilation rate (A_C) and air temperature (T_a) along with statistical information of the variability observed within 30–31 day long periods. Data from both 1999 and 2000 have been pooled and the data show little difference in maximum, minimum and median I diurnal patterns from mid-April to mid-August. Median I values decline thereafter, though maximum

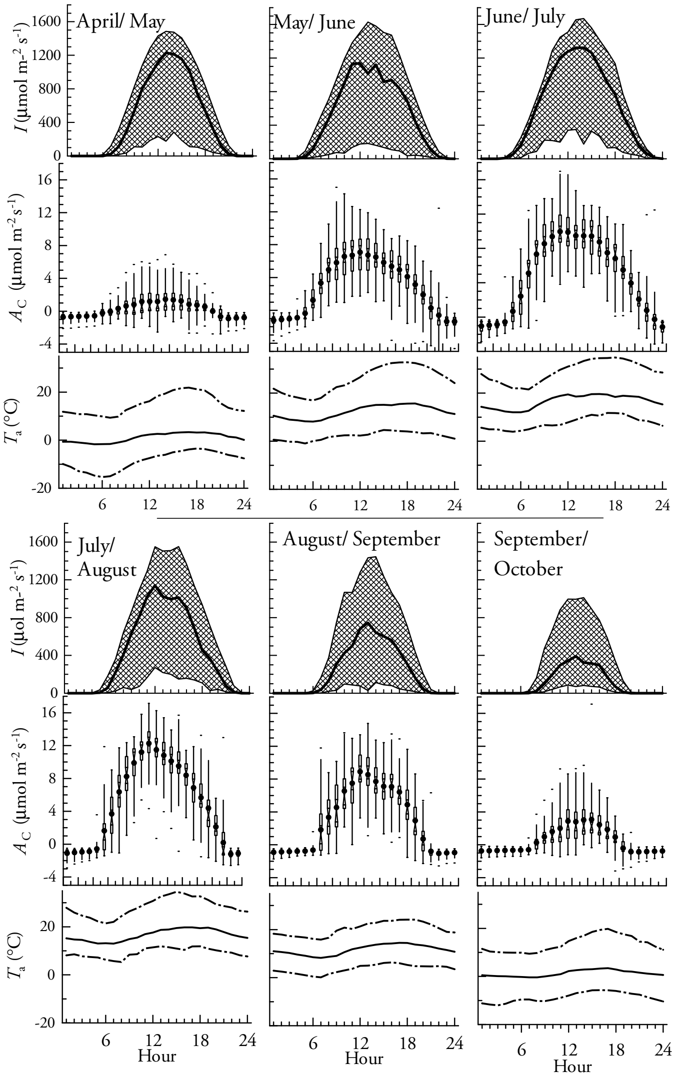

Fig. 1. Seasonal pattern of diurnal variations of photosynthetically active radiation (I), canopy net CO_2 assimilation rate (A_C), and air temperature (T_a). Six periods, each of 30 or 31 days, from the 16th day of a the first month to the 15th day of the subsequent month are shown, and data from both 1999 and 2000 have been pooled for this analysis. For I, the shaded area encompasses the maximum and minimum hourly average values observed for each hour, with the solid line representing the median diurnal pattern. For A a more comprehensive data description of hourly variations is given. The sold circle represents the arithmetic mean with the bases of the triangle and upside-down triangle representing the upper and lower notches (equal to $M \pm 1.58i/n$, where M is the median value, i is the interquartile range and n is the number of observations), the triangles joining at the median value. The rectangles beyond the triangles extend to the 0.75 and 0.25 quartiles (above and below the median respectively) with the solid lines extending from the rectangles for an extra length representing $1.5i$. The upper and lower dashes represent the extreme maximum and minimum values observed. For T_{air} the maximum and minimum hourly values are indicated by dashed lines, with the median diurnal pattern for the period shown by the solid line.

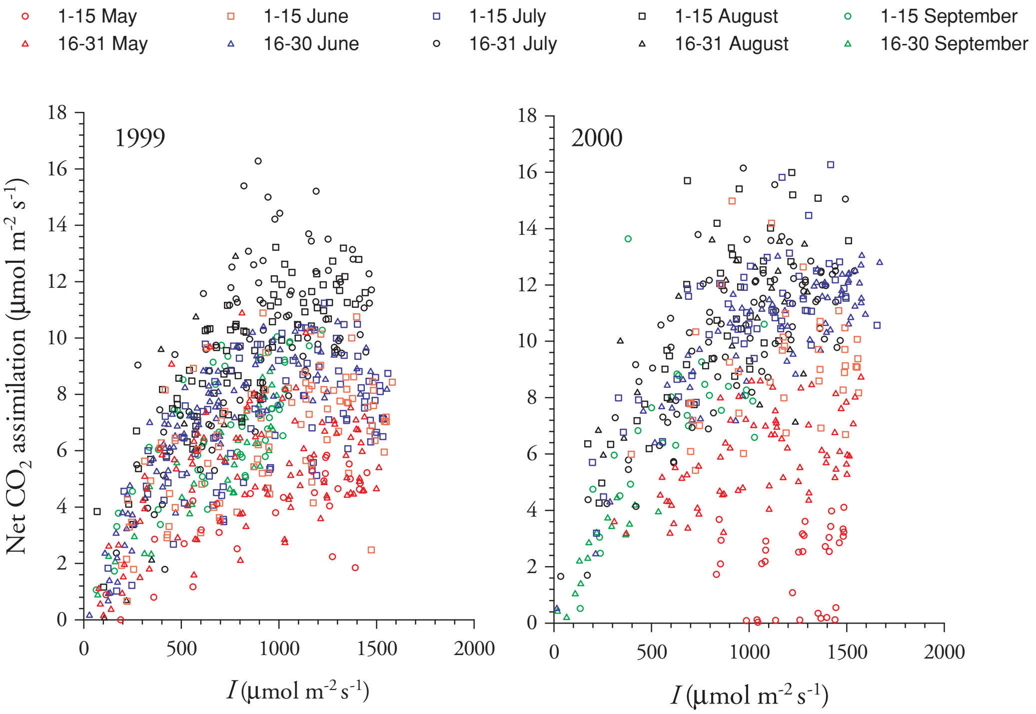

Fig. 2. The response of canopy net CO_2 assimilation rate to incoming photosyntheticaly active radiation (I), grouped into periods of 15–16 days for 1999 and 2000.

values less markedly. This pattern reflected both the decreasing solar angle and increased cloudiness as autumn approached.

Despite the similar overall diurnal patterns in I from mid-April to mid-August, large changes in canopy assimilation characteristics were observed over this period. For April/May the maximum median A was only about 1.5 μmol m^{-2} s^{-1}, whereas for May/June it was already 7 μmol m^{-2} s^{-1}. These maximum values increased to 12.5 μmol m^{-2} s^{-1} in July/August, after which they declined rapidly, being only around 3 μmol m^{-2} s^{-1} in September/October. Figure 1 also shows changes in the overall shape of the diurnal pattern. Although more or less coincident with the daily trend in I for April/May and from mid-August to mid-October, during the warmer late Spring/Summer period both median and maximum observed A typically peaked several hours prior to solar noon (ca. 1300 h).

Despite large variations in average diurnal patterns throughout the growing season (this being defined here as the period of any measurable photosynthetic activity), the magnitude of day-to-day variations was not substantially smaller in April/May or September/October compared to the summer months. This was despite much reduced average fluxes. Both positive and negative A_C (the latter indicating daytime canopy respiration) were observed on occasions during the middle of the day at both ends of the growing season.

Air-temperature data are shown mainly for information, but also illustrate the high degree of day-to-day variability in this continental environment. This is particularly marked at either end of the growing season where, for any given time of day, temperatures can vary as much as 30 °C within a 30/31 day period. For both April/May and September/October it is also worth pointing out that on some occasions even midday temperatures remained below 0 °C.

Though perhaps not aesthetic to the eye, Fig. 2 serves to illustrate the actual variability in measured fluxes. It is designed to show the effect of time of year on the A_C versus I relationship and to illustrate differences between 1999 and 2000. Firstly for 1999, it can be seen that quite early on in the growing season (after around 1 June) the initial slope of the canopy light response curve was already very close to the maximum summer value. In contrast to this, light-saturated rates continued to increase until late July. It can also be seen that during September, the initial slope and perhaps the maximum rate were again lower than the summer months.

For 2000, A_C was much lower that 1999 early on in the growing season, especially the period 1–15 May. This was a consequence of lower air temperatures and a much later snow melt than in 1999. Generally speaking, however, similar overall patterns were observed for 1999 and 2000, with light saturated rates tending to be greatest in August in both years. Overall for the period 1 June to 15 August CO_2 assimilation rates at any given I were slightly higher in 2000 than in 1999. This difference was already evident quite early on in the growing season, and occurred despite the later commencement of photosynthetic activity in 2000.

For both 1999 and 2000, there are clear indications of some decline in photosynthetic rates during September. The underlying basis of this phenomenon is investigated in Figs. 3 and 4. Figure 3 documents the changes in I (Fig. 3a), gross primary productivity, G_P (the terminology used here for the photosynthetic integral, positive terms only, at scales of one day or more; see Section 2.5) (Fig. 3b), and air temperatures (Fig. 3c) for the period 1 August to 15 October for both 1999 and 2000. Not surprisingly, all three parameters show a decline during this period with similar patterns in both years. Importantly, the decline in G_P is more rapid than is the decline in I. This implies that there are some other environmental factors or perhaps some changes in plant physiology acting to reduce G_P during this time.

From Fig. 3a and Fig. 3c, it is clear that superimposed on the longer term decline is significant day-to-day variability in both incoming insolation and air temperatures. In order to glean information on the underlying causes of the rapid photosynthetic decline, we have therefore utilised this day-to day variation by selecting days during the period shown in Fig. 3 in both 1999 and 2000 with a reasonably high incoming I and without vastly dissimilar daytime temperatures. These are indicated in Fig. 3c with the associated A_C versus I relationship (hourly values; quality-controlled data only) shown in Fig. 4.

For 1999, Fig. 4a shows drastically different light response curves observed during this period. Firstly, the canopy light response curves of 27/28 August are typical of those observed for the 30 previous days (not shown, but see Fig. 3a). Nevertheless, only 15 days later substantially lower A_C at all I were observed (12/13 September). This was despite very similar temperatures to those occurring in late August (Fig. 3c). The light response of the forest on 20/21 September was indistinguishable from that on 12/13 September with similar temperature regimes again occurring on those days. Following a period of colder weather and one sunny day with a maximum temperature of only -2.8 °C (26 September, day 269) an unusually warm period followed with maximum temperatures around 14 °C for 5 and 6 October. Despite these favorable environmental conditions, A_C was always less than 2 μmol m^{-2} s^{-1} on both days, even at $I > 700$ μmol m^{-2} s^{-1}.

For 1999 photosynthetic data for the period 31 August to 7 September are missing due to instrumental problems (Fig. 3b). No such problem exists for 2000, and these data suggest two phases for the initial photosynthetic decline. Curves for 2 and 6 September 2000 show that, initially, it is only at higher I that decreased photosynthetic rates are observed. Subsequently, the initial slope declines and canopy light response curves similar to the same period in 1999 were then observed until 28 September. As for 1999, after a cold and chilly period (4–8 October) and despite warmer temperatures again (above 3 °C on 13 October 2000) A_C was never greater than 2 μmol m^{-2} s^{-1}.

3.2. Relationships between canopy conductance and canopy CO_2 assimilation

Although much of the variation in A_C over the time period from 1 June to 31 August can be accounted for by natural variations in I, substantial "noise" in the data is still apparent (see Fig. 2). One possibile means to account for this is through changes in canopy stomatal conductance (G_c) with canopy-to-air vapour pressure difference, D_c (Tchebakova et al., 2002). This is examined in Fig. 5, where the response of both A and G_c to D_c are examined for high light conditions ($I > 1000$ μmol m^{-2} s^{-1}). For 1999 G_c decreased markedly with D_c for all time periods examined, but for any D_c, G_c was substantially lower earlier on in the growing season. Similar general patterns in the response of G_c to D_c were observed for 2000, except for the period 1–15 May, which was the period of a slower recovery from the quiescent to the physiologically active stage due to lower air temperatures in 2000.

Substantial declines in A with D_c were also observed in both years, with sharp differences in rates early on (here circled) also apparent. Figure 5 also more clearly

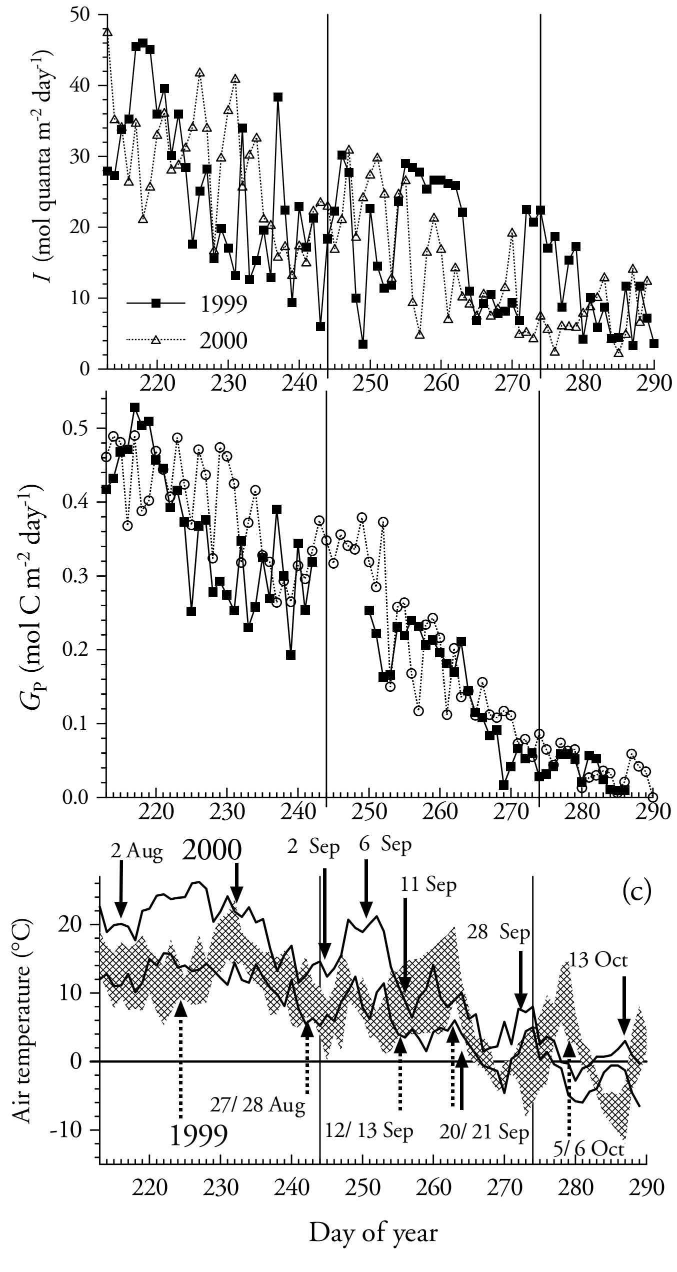

Fig. 3. Changes in (a) incoming photosynthetically active radiation (I), (b) gross primary productivity (G_P) and (c) minimum and maximum air temperatures from 1 August to 15 October in 1999 and 2000. Also shown in Fig. 3c are the days used for more detailed analysis of the A versus I response in Fig. 4.

shows the higher canopy photosynthetic rates in 2000 cf. 1999, especially so for early June.

Figure 5 clearly implies that a substantial stomatal limitation on rates of carbon acquisition occurred for this forest, at least under conditions of high I, except for the earliest stages of the growing season. (It should be noted that due to substantially lower I after 15 August, such an analysis was not possible in autumn). One

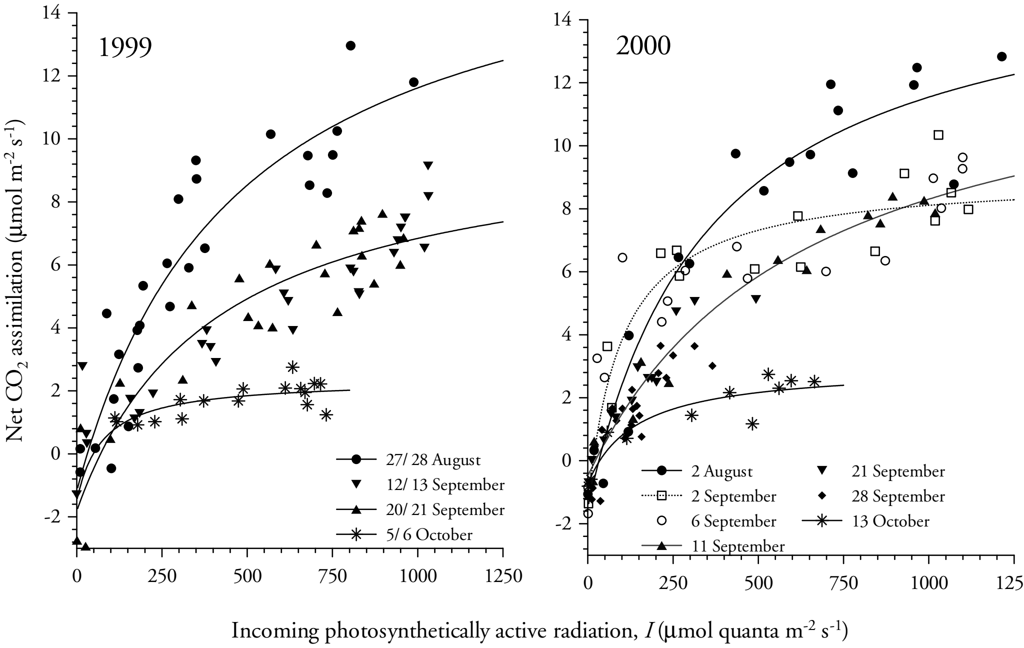

Fig. 4. The response of canopy net CO_2 assimilation rate to incoming photosyntheticaly active radiation (I) in late summer and autumn for 1999 and 2000. Days presented for each year have been chosen on the basis of a high maximum I, good data quality and, as far as possible, similar temperatures within in each year.

approach to quantify the relationship between stomatal conductance and photosynthesis sometimes applied at the leaf level is the theory of Cowan (1977). He hypothesized that stomata should serve to optimise the marginal water cost of plant carbon in such a way that

$$\frac{\partial E}{\partial A} = \lambda, \tag{9}$$

where λ is a Lagrange multiplier that must remain constant over periods of one day or more. Although the direct scaling of such relationships to the canopy level is not straight forward (see McNaughton, 1994 and Grace et al., 1998), Lloyd et al. (1995) applied this relationship at the canopy level, using the analysis of Lloyd (1991) and Lloyd and Farquhar (1994) to show that for constant λ the simple relationship

$$G_c = \frac{A_C\lambda^{0.5}}{[D_c(C_a - \Gamma)/1.6]^{0.5}}, \tag{10}$$

should hold. Here C_a is the ambient carbon dioxide concentration and Γ is the CO_2 compensation point. This means that a plot of G_c versus $A_C/[D_c(C_a - \Gamma)/1.6]^{0.5}$ should yield a slope equivalent to $\lambda^{0.5}$. Such plots are shown in Fig. 6 for both 1999 and 2000, where all available quality controlled data have been included for both years. This shows that, especially when considering the numerous possible errors involved in the estimation of G_c [eq. (4)–(6)] that λ does appear to be reasonably constant throughout the growing season for both years. Somewhat remarkably though the slopes for the two years are significantly different at the 95% level; being 20.4 ± 7.1 in 1999 and 28.5 ± 11.4 in 2000. This suggests best estimates for λ of 416 mol mol^{-1} in 1999 but 815 mol mol^{-1} in 2000. Even more surprisingly, these year-to-year differences are apparent from the earliest days of the onset of photosynthetic activity in spring (!). From the theory of Cowan (1977) this implies that the Zotino forest was more "aggressive" in its water use in 2000 as compared to 1999.

From Figs. 5 and 6 the question then emerges as to whether or not the higher canopy photosynthetic rates in 2000 cf. 1999 were just a consequence of higher canopy conductances as evidenced by a higher λ, or whether or not some increase in canopy (chloroplast) photosynthetic capacity was also involved. One approach to this problem is to examine the relationship between G_c and A_C and such a plot for high light conditions is shown for the period 15 June–15 July in Fig. 7.

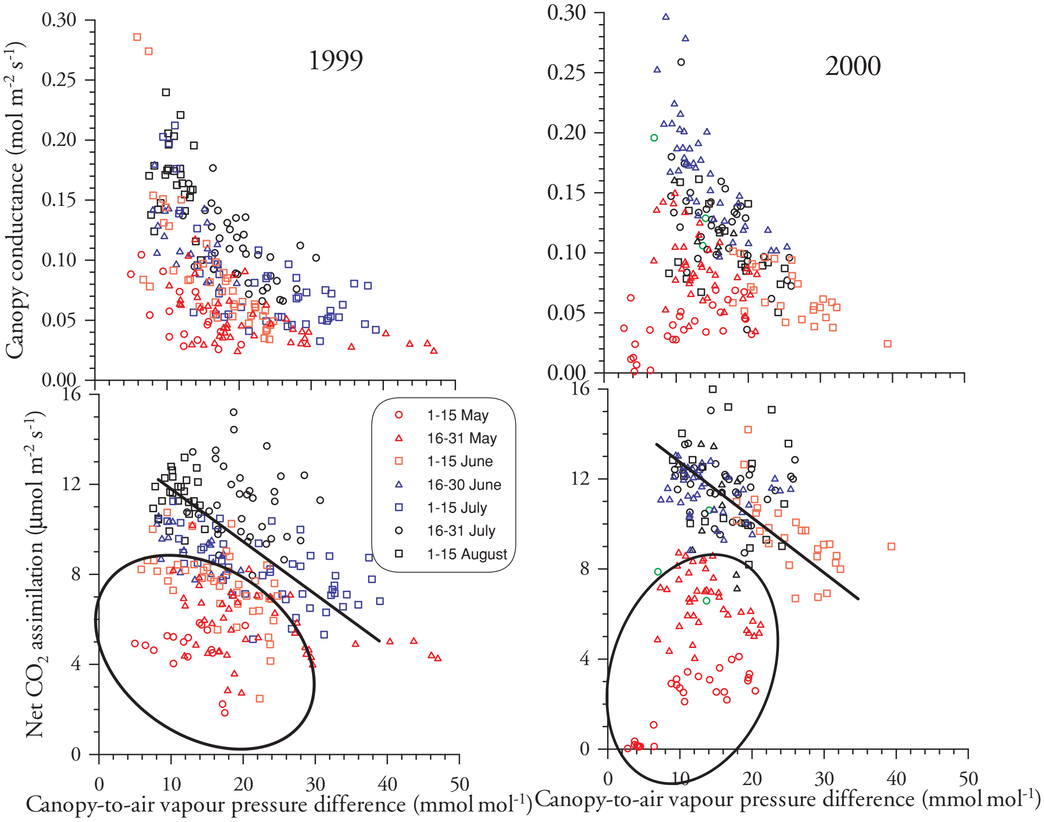

Fig. 5. The response of canopy stomatal conductance and canopy net CO$_2$ assimilation rate to canopy-to-air vapour pressure difference in 1999 and 2000. Data have been grouped into periods of 15–16 days, and for CO$_2$ assimilation data associated with the early springtime recovery are circled. Data used is only that from high light ($I > 1000$ μmol m^{-2} s^{-1}) conditions.

Also shown are fitted curves for both years, calculated according to a simple model of a linear dependence of photosynthesis on chloroplastic CO$_2$ partial pressure, C_c, and including the combined effects of G_c and A_C on C$_c$ according to

$$A_C = \frac{k(C_a - \Gamma)}{1 + k/G_c}, \tag{11}$$

where k is the canopy carboxylation efficiency. The fitted curves give estimates of $k = 0.056$ mol m^{-2} s^{-1} bar^{-1} for 1999 and $k = 0.062$ mol m^{-2} s^{-1} bar^{-1} for 2000. This suggests that as well as a higher λ (and hence by virtue a higher G_C under equivalent environmental conditions), higher photosynthetic rates in 2000 were also attributable to a slightly higher photosynthetic capacity.

3.3. *Photosynthesis, respiration and the net ecosystem carbon balance*

The above analysis has concentrated on canopy photosynthetic rates or gross primary productivity (G_P) as deduced from measurements of net ecosystem exchange (N_E) and estimates of ecosystem respiration rate, R_E (Shibistova et al., 2002b). Figure 8 thus summarises the overall patterns observed for these three canopy gas exchange parameters, the seasonal patterns in the daily I integral, and daily average soil and air temperatures and rainfall for the entire study period. Here we have made the assumption, based on likely relationships between cambial activity and xylem elements development (as evidenced by tree-ring sections) and stem respiration rates, that for 1998 intrinsic rates of stem respiration would have been similar to those for 2000 (Shibistova et al., 2002b).

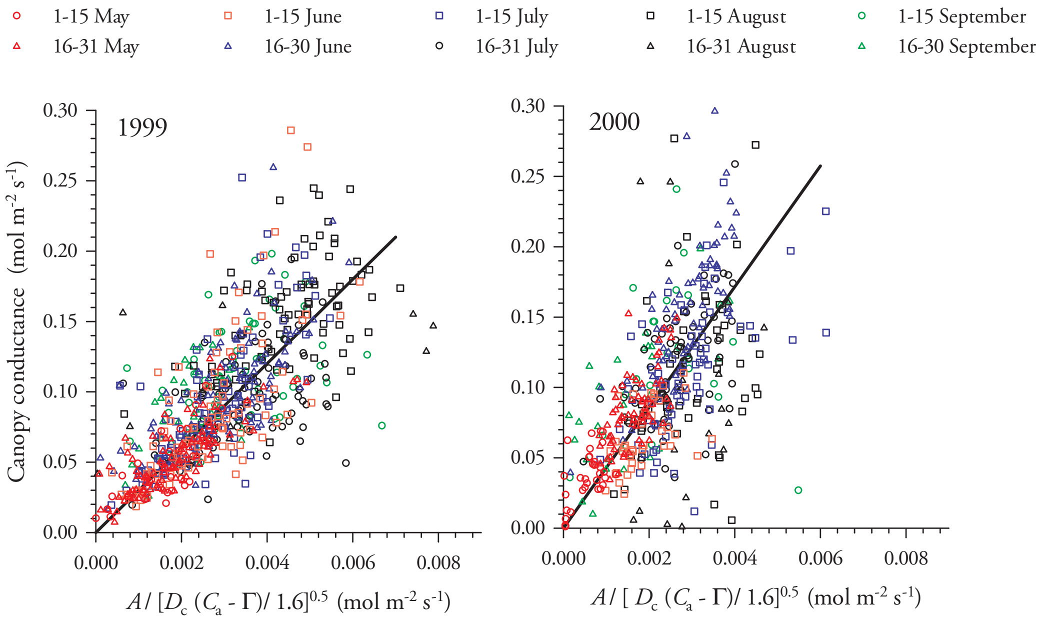

Fig. 6. The response of canopy conductance to a multiplicand involving net CO_2 assimilation (A_C), canopy-to-air vapour pressure difference (D_C) ambient CO_2 concentration (C_a) and the CO_2 compensation point (Γ). According to eq. (10) such a plot should yield a straight line with intercept zero and slope equal to $\lambda^{0.5}$, where λ is a Lagrange multiplier describing the maginal evaporative cost of plan carbon gain.

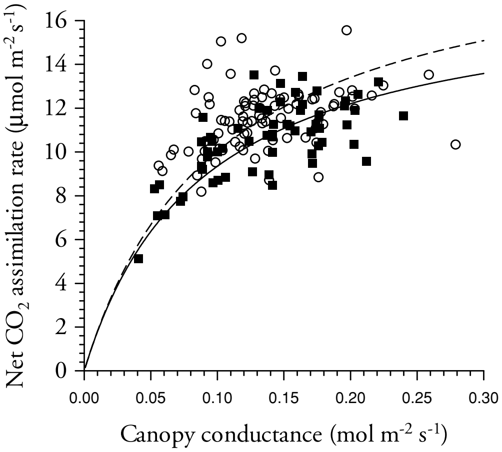

Fig. 7. The relationship between canopy net CO_2 assimilation rate and canopy stomatal conductance for July 1999 and July 2000. Also shown are non-linear least-squares fit to eq. (11).

In any case, stem respiration typically constitutes only a small component of the ecosystem respiratory flux (Shibistova et al., 2002b) and any errors in the partitioning of N_E for 1998 in Fig. 8 should not be large.

Figure 8 shows that on almost every day of the growing season (more or less May to September), N_E was negative implying net accumulation of carbon by the ecosystem. For the period when G_P was sizeably >0, the only time where $R_E > G_P$ was for a brief period in late September/early October (Fig. 8b) when soil temperatures were still substantially above zero (see Shibistova et al. 2002a for more detailed information), but photosynthesis had declined nearly to zero after the first daytime frosts (Fig. 3). Some respiratory flux was evident throughout the colder months (November to April) when 5 cm depth soil temperatures remained above −5 °C despite air temperatures rarely, if ever, going above zero, sometimes being as low as −52 °C (see also Shibistova et al., 2002a,b). As a result, winter-time R_E was slightly positive (typically 0.05 mol C m^{-2} d^{-1}) but this was not nearly of sufficient magnitude to offset the much larger net carbon uptake that occured through almost all of the growing season. Thus, the overall annual net primary productivity ($-N_E$) of the Zotino forest is substantial, being estimated here at 12.1 mol C m^{-2} a^{-1} for 1999 and 13.6 mol C m^{-2} a^{-1} for 2000. Using the “maximum data” estimates for R_E of Shibistova et al. (2002b) of 34.5 mol C m^{-2} a^{-1} and for 1999 and 38.7 mol C

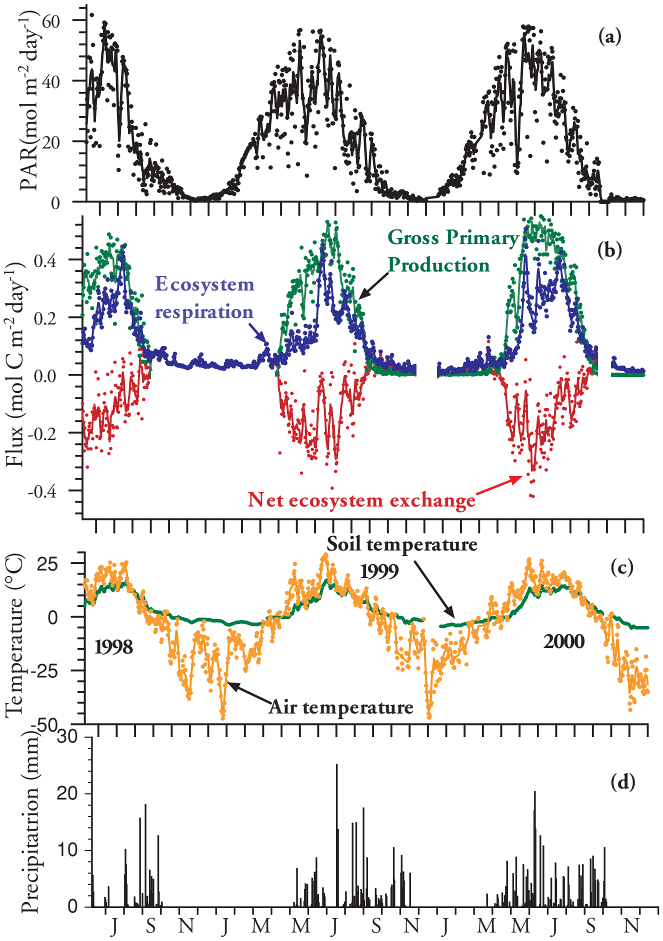

Fig. 8. The seasonal pattern of (1) daily PAR integral, gross primary productivity, ecosystem respiration and net ecosystem exchange rate from 7 June 1998 to 31 December 2000 for the Zotino stand. Also shown are daily average soil and air temperatures and precipitation where falling as rain.

m^{-2} a^{-1} for 2000, the associated G_P are 46.6 mol C m^{-2} a^{-1} and for 1999 and 52.3 mol C m^{-2} a^{-1} for 2000.

3.4. Components of the net ecosystem carbon balance

In what follows, we estimate the main flows of carbon within the Zotino forest by combining our estimates of G_P, R_E and N_E with the biomass inventory and tree ring increment analyses in the same forest by Wirth et al. (1999, 2002a,b,c). Table 1 shows the relevant estimates of plant carbon density, plant carbon increment, net primary productivity and the net rate of loss for leaves, branches, boles, coarse roots and fine roots and their total.

We first infer the rate of root respiration according to

$$R_r = G_P - R_f - R_{st} - N_P,$$

where R_r is the rate of respiration by roots, R_{st} is the rate of respiration by stems and N_P is the net primary productivity. Using the average (1999 and 2000) G_P estimate of 49.5 mol C m^{-2} a^{-1} and averaged estimates (1999 and 2000) for R_f and R_{st} of 6.8 mol C m^{-2} a^{-1} and 8.2 mol C m^{-2} a^{-1} (Shibistova et al., 2002b), and the N_P estimate of 17.7 mol C m^{-2} a^{-1} we obtain R_r = 16.8 mol C m^{-2} a^{-1}. This gives a

Table 1. *Carbon density, net primary productivity, litterfall and mortality and the net rate of increase in carbon density for the Zotino forest*[a]

Component	Carbon density (mol C m^{-2})	Net primary productivity (mol C m^{-2} a^{-1})	Litterfall and mortality (mol C m^{-2} a^{-1})	Rate of increase (mol C m^{-2} a^{-1})
Foliage	19.6	3.7	3.7	0
Twigs	4.5	0.6	0.6	0
Branches	61.5	0.7	0.5	0.2
Bark	33.5	0.2	0.2	0.1
Boles	390.5	2.8	0.4	2.3
Coarse roots	104.9	0.4	0.2	0.2
Fine roots	18.7	9.4	9.4	0
TOTAL	633.2	17.7	14.9	2.8

[a] Data come from the work of Wirth et al. (1999, 2002a,b,c) with some site-specific revisions. In particular, fine root productivity is now estimated to be higher than in Wirth et al. (2001b) on the basis of a 2-yr turnover time and a sampling of 100 1 m depth soil cores in a 1 ha area around the forest tower in 2001 (Shibistova, Lloyd, Zrazhevskaya, Iliin, Savushkina, Santos, Zolotoukhine, Santoshinka, Dolgushin and Karat; unpublished data). Stem mortality has been estimated on the basis of the measured density of dead trees assuming a mean "lifetime" for standing dead trees of 30 yr (Wirth, 2000).

total plant (autotrophic) respiration rate of 31.7 mol C m^{-2} a^{-1} and an estimated proportion of photosynthesis utilised in respiration rather than growth (φ) of 0.64.

We use the estimate for "soil respiration" of Shibistova et al. (2002b), R_s, noting also that this is based on ground-level eddy covariance measurements and thus includes any CO_2 respiring from decaying coarse woody debris (CWD) and any small net annual carbon gain by the lichen layer. This allows us to infer the rate of heterotrophic respiration of soil and coarse woody debris microbiota, R_{mic}, according to

$$R_{mic} = R_s - R_r,$$

from which we estimate R_{mic} to be only 4.7 mol C m^{-2} a^{-1}.

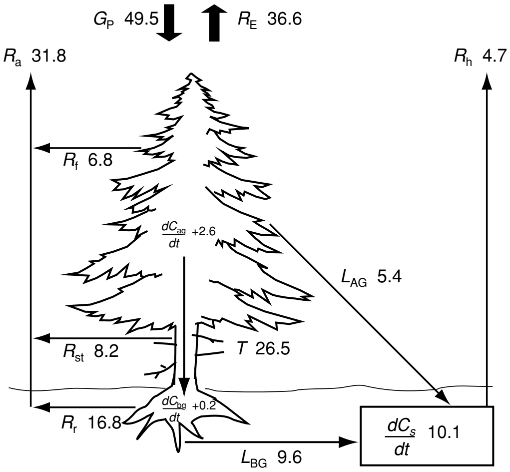

Fig. 9. Estimated annual total carbon flows for Zotino stand. All units are in mol C m^{-2} a^{-1}. The data sources are described in Table 1. G_P, gross primary productivity; R_E, total respiration; R_{st}, stem respiration, R_r, root respiration, R_a, autotrophic respiration; R_h, heterotrophic respiration; L_{AG}, above-ground losses (litterfall and mortaliy); L_{BG}, below-ground losses (root mortality, fine root turnover and exudation); T, below-ground C translocation; dC_{ag}/dt, rate of change in above ground carbon density; dC_{bg}/dt, rate of change in belowground carbon density; dC_s dt, rate of change in soil carbon pool. Figure design based on Malhi et al. (1999).

From an estimate of the rate of entry of plant material into the soil organic carbon and CWD pools ($L_P = 14.9$ mol C m^{-2} a^{-1}; Table 1) the rate of accumulation of carbon in soil and CWD can then be estimated as

$$\frac{dC_s}{dt} = L_P - R_{mic},$$

where C_s is the density of soil carbon (including fine litter) and CWD. This suggests a high rate of net carbon accumulation in the soil and CWD pool of 10.1 mol C m^{-2} a^{-1}, much higher than the estimates of the rate of accumulation of carbon in plant material above ground ($dC_{ag}/dt = 2.6$ mol C m^{-2} a^{-1}) and below ground $dC_{bg}/dt = 0.2$ mol C m^{-2} a^{-1}). All component fluxes by this calculation (which must, by its nature be "closed") are shown in Fig. 9. The residual term in this calculation involves the flow of carbon from the roots to the soil carbon pool. This includes fine and coarse root turnover as well as any losses of carbon as root exudates. At 9.6 mol C m^{-2} a^{-1} it emerges as the main flow of plant matter into the soil carbon pool in this calculation. Heterotrophic respiration, according to this scheme, accounts for only about 12% of the ecosystem total.

4. Discussion

The analysis here considers both the overall net exchange of carbon by the canopy (N_E) and the magnitude and environmental modulation of the canopy assimilation of CO_2 of the foliage, estimates of the latter being obtained using estimates of ecosystem respiration outlined in an accompanying paper (Shibistova et al., 2002b). That paper also discusses, in detail, flux corrections for both the above and below canopy eddy covariance systems, particularly those associated with low turbulence intensities at night. We believe that, according to current knowledge, our flux estimates are as reliable as possible.

Examination of the changing diurnal patterns of CO_2 assimilation (A_C) during the growing season (Fig. 1) showed very low rates in April/May around the time of snow melt until ambient air temperatures rose above about 0 °C. During spring, however, photosynthesis could recover rapidly from <0.2 μmol m^{-2} s^{-1} to reasonably "normal" growing season rates (ca. 6 μmol m^{-2} s^{-1}) in time periods as short as one week (see for example the first week of May in 1999; days 121–128; Fig. 8). Figures 1 and 2 also show a continued but slower increase in photosynthetic capacity throughout the growing season. This does not seem to be a simple temperature effect on photosynthesis, as maximum light-saturated photosynthetic rates were observed in August for both years despite temperatures in that month being substantially lower than for July in both 1999 and 2000. For example, daily average temperatures in 1999 for June, July and August were 10.4, 17.9 and 12.6 °C, respectively, and for the same three months in 2000 they were 16.6, 16.1 and 13.2 °C. This suggests that rather than being due to differences in ambient temperatures, the seasonal pattern in light saturated rates observed in both years was more related to some change in intrinsic photosynthetic capacity during the growing season.

The pattern described above may thus indicate two phases in the recovery of photosynthesis in spring and early summer, the first involving a major reorganisation of the antenna complexes from stable aggregates with a maximized capacity to dissipate absorbed heat such as persists in boreal Scots pine throughout the winter (Ottander et al., 1995), with a second slower phase, probably associated with new chlorophyll synthesis, during late spring and early summer (Ottander et al., 1995; Nichol et al., 2002). Consistent with the latter explanation is that the forest quantum yield, an indicator of photosynthetic efficiency rather than total light harvesting ability, tended to recover faster than the light saturated rate (Fig. 2). Also involved in the slower increase in photosynthetic capacity during summer may be changes in leaf area associated with new needle production which occurs at our site in July and August (A. A. Dolgushin, unpublished observations). Overall, however, pine needles are quite long-lived in Siberia, with the data of Table 1 suggesting a mean lifetime of around 5 yr. So only minor changes in total canopy leaf area might therefore be expected during the growing season. Shibistova et al. (2002b) have estimated the respiratory costs associated with new needle production. They concluded that they are small (<0.1 μmol m^{-2} s^{-1}), with only minimal effects on the daytime canopy carbon balance.

In addition to being a consequence of decreasing I during autumn, a close analysis of the decline in G_P around this time (Fig. 3) showed that a decrease in the canopy photosynthetic capacity was also involved. From data in 1999 and 2000 (Fig. 4) we may infer that there seems to be at least three stages in this process; the first involving a decrease in the light-saturated rate, the second involving a decrease in canopy quantum yield and the final phase, associated in both years with the first daytime frosts on sunny days, involving a large, apparently irreversible (or very slowly reversible) reduction in photosynthetic capacity at all I.

The initial reduction in the light-saturated rate is consistent with the growth chamber studies of Öquist et al. (1980), who observed that the maximum electron transport rate of isolated chloroplasts was reduced prior to any reduction in chloroplast photosystem-II (PSII) capacity during the early stages of the autumnal hardening process. This was also seen in the work of Vogg et al. (1998), who observed an initial reduction in chlorophyll and inferred PS-II reaction centre number for Scots pine growing outdoors near Bayreuth (Germany) during autumn and winter. Those workers also showed that this was a photoperiodic response, and most recently, Savitch et al. (2002) have suggested that the subsequent decline in quantum yield may be attributable to a feedback inhibition on photosynthesis due to the photoperiodically controlled termination of growth in autumn. Importantly, this photosynthetic down-regulation is perhaps intricately linked to the hardening process prior to the winter. Also involved in this photosynthetic down-regulation may be the increased mobilisation of starch reserves that typically occurs in conifers during autumn (Erickson, 1979; Sudachkova et al., 1994). This perhaps occurs just as a consequence of longer night lengths as autumn approaches. Starch degradation in leaves typically occurs only at night or at low light (Kossmann and Lloyd, 2000) and recently Paul and Foyer (2001) have suggested that increased sugars from starch turnover may be important in the down regulation of photosynthetic gene expression.

Although Figs. 1 and 2 suggest a dominant role of I in affecting the rate of carbon acquisition by the forest during summer, high canopy-to-air vapour pressure deficits also exerted a strong effect on canopy A, presumably through their effects on stomatal closure (Fig. 5). Such stomatal responses to D_C are well documented for plants in general, and may be especially strong in coniferous plants (Lloyd and Farquhar, 1994). They have also been observed from stand-level eddy covariance studies for a boreal jack pine (*Pinus banksiana*) stand growing in Canada (Baldocchi et al., 1997).

One framework from which to view this stomatal response is the optimisation theory of Cowan (1977), in which the inferred value of λ gives an indication of the nature of the canopy water-use strategy in terms of possible carbon gains, a low λ indicating conservative water use and vice versa. This theory has been tested in the field for Scots pine in Finland (Hari et al., 1999) and seems to hold remarkably well at the shoot level. From Fig. 6, especially when taking account the many parameters needed for the estimation of canopy conductance [eqs. (4)–(6)] and hence potential errors in its estimation, we may also conclude that at the canopy level stomatal behaviour of Siberian Scots pine is in accordance with that hypothesis, This was also shown to be the case for *Larix gmelinii* growing in eastern Siberia (Hollinger et al., 1998). The values obtained here (viz. $\lambda = 415$ mol mol^{-1} in 1999 and $\lambda = 816$ mol mol^{-1} in 2000) are, however, substantially greater than the values found for Scots pine in Finland (about 175 mol mol^{-1}; Hari et al., 1999) suggesting a more aggressive water use by the Siberian stand than is the case for this species growing in cooler more maritime environments. The underlying reasons for this are unclear. However, it does seem to fit with the general pattern of plant water-use strategy pointed out by Lloyd and Farquhar (1994), viz. that when evaporative demand is high (as it is in Siberia), the more successful plants are those that have a non-conservative water use strategy.

Quite remarkably, although reasonably constant in both years, λ was nearly two-fold higher in 2000 as compared to 1999. The underlying reasons for this can only be speculative at this stage. There may, however, be a common link with the slightly higher photosynthetic capacity also evident for the forest in 2000 (Fig. 7). For example, stem growth rates were much reduced in 1999 as compared to 1998 and 2000, probably due to much lower than usual air temperatures early on in the growing season in that year (Shibistova et al., 2002b). Perhaps this may have freed up carbohydrates allowing for higher than usual rates of fine root growth in the 1999 growing season, with subsequent possibilities for higher nutrient uptake and less conservative water use from early on in 2000. From what evidence is available, it seems that substantial year-to-year variations in fine root production can occur for boreal Scots pine trees (Makonnen and Helmisaari, 2001). It is unlikely that canopy photosynthetic characteristics and their response to the environment would not in some way be affected by any large variations in the amount of fine root mass present.

The G_P of the Siberian forest of 46.6 mol C m^{-2} a^{-1} for 1999 and 52.3 mol C m^{-2} a^{-1} for 2000 are relatively low when compared to boreal forests in Europe. For example, from data summarised by Valentini et al. (2000) G_P has been estimated at around 100 mol C m^{-2} a^{-1} for two stands in Sweden and around 85 mol C m^{-2} a^{-1} for a 30-year-old regenerating stand in southern Finland. For a mixed spruce stand in European Russia. Milyukova et al. (2002) estimated G_P to be 122 and 130 mol C m^{-2} a^{-1} for 1999 and 2000, respectively.

The projected LAI of the European boreal forests reported above is typically around 4 (Valentini et al., 2000; Milyukova et al., 2002). This is opposed to about 1.5 for the Siberian forest studied here. This difference provides one explanation for the contrasts in photosynthetic productivity between the European and Siberian boreal forests studied to date. This is especially the case as one might expect a positive feedback between LAI and G_P: higher photosynthetic rates giving rise to more available carbon for plant growth and hence more potential leaf area; that giving rise to more radiation interception by the canopy and hence higher canopy photosynthetic rates (and so on). Perhaps the generally milder European summers with less evaporative demand and less likelihood of severe soil water deficits (Kelliher et al., 2001) are important in allowing forest stands there to have a higher LAI and G_P. This idea gains support from the strong negative effect of D_C on the stand carbon balance in Siberia (Fig. 5), as well as some evidence of adverse effects of summer soil water deficit on the water use and productivity of *P. sylvestris* in central Siberia (Arbatskaya and Vaganov, 1997; Kelliher et al., 1999; Arneth et al., 2002).

The extent to which soil water deficits *per se* reduced the canopy conductance and photosynthetic productivity of the measurement stand during the period examined here is, however, unclear. For example, Tchebakova et al.(2002) found that during a 3 wk dry period in July 1998 there was no evidence of adverse effects of soil water deficits on the canopy conductance. This was despite the extremely low water holding capacity of the sandy soil substrate. This was attributed to the forest accessing water from a perched water table at about 2 m depth. By contrast, when modelling the long-term trend in the isotopic composition of growth-rings from trees growing in the same forest as studied here, Arneth et al. (2002) found that their model fit was much improved by inclusion of simple hydrological module which allowed for some stomatal closure as the soil dried out. One possibility to account for this discrepancy is that variations in the winter snow fall and snow melt timing might affect the height and hence the subsequent accessibility of the watertable during low rainfall periods when the upper soil layers may be become extremely dry (Tchebakova et al., 2002). Examination of snow depth data for the nearby town of Vorogovo show an unusually late snow melt to have occurred in 1998; the main year of the Tchebakova study.

Although lower than for the boreal forests of Europe, the G_P estimates here are comparable to the boreal forests of Canada. For example, for four relatively mature coniferous forests studied as part of the BOREAS study, Ryan et al. (1997) obtained estimates of 60 ± 10 mol C m^{-2} a^{-1}. As for the forest studied here, there seems to little direct evidence of any strong adverse effects of soil water deficit on the Canadian boreal forest carbon balance (Baldocchi et al., 1997; Goulden et al., 1997; Jarvis et al., 1997). Moreover, G_P seems similar despite the Canadian forests having a greater LAI than is typical for *P. sylvestris* in central Siberia (Chen et al., 1997; Schulze et al., 1999; Wirth et al., 1999). Perhaps differences in nutrient availability as reflected in foliar N content are important. Such data are available for both Canadian and Siberia forests (Dang et al., 1997; Wirth et al., 2001a), but different sampling and pooling methodologies make direct comparisons difficult. A second possibility is that differences in summer insolation are important, Generally speaking Canadian forests are at a lower latitudes than their Siberian counterparts and thus probably receive less I during the summer months. From Figs. 1 and 2 we may conclude that such differences in I might have important consequences for canopy productivity.

Another interesting comparison is the ratio of above-ground net primary productivity, $N_{P(AG)}$, to G_P. For the Siberian stand studied here the former has been calculated to be only about 8 mol C m^{-2} a^{-1} (Wirth et al., 2002b; Table 1). This gives a ratio of $N_{P(AG)}$ to G_P of about 0.15, a value that is almost certainly lower than Canadian boreal forests studied so far (Ryan et al., 1997). This suggests extensive allocation of carbon resources below-ground in Siberian forests (Schulze et al., 1999) and/or unusually high maintenance respiratory costs.

We have been able to quantify the latter, by virtue of below canopy eddy covariance measurements and measurements of N_P (Table 1), and the value of the proportion of G_P lost as autotrophic respiration (φ) is estimated here at 0.64. This is comparable to estimates for boreal coniferous forests in Canada (Baldocchi et al., 1997; Ryan et al., 1997). On balance, these estimates of φ for boreal forests seem higher than for most temperate forests (Waring et al., 1998). This might be expected on the basis of boreal forests being typically slow growing and having a more limited nutrient availability (Van der Werf et al., 1994).

Lloyd and Farquhar (1996) and Lloyd and Farquhar (2000) have argued that a high ecosystem φ should be associated with relatively strong responses of ecosystem N_P to the currently increasing concentrations of atmospheric CO_2, although for nutrient-poor plants this effect may be offset by an inability to take up the extra nutrients to support faster growth rates. However, even when their use of a lower φ than now seems appropriate for boreal forests is taken into account, the theoretical analyses of Lloyd and Farquhar (1996) and Lloyd (1999b) suggest that at the current time the net accumulation of carbon by boreal forests in response to increasing atmospheric CO_2 concentrations should be at most 2 mol C m^{-2} a^{-1} in the absence of any nutrient limitations and at most 1 mol C m^{-2} $a^{-1}$when nitrogen limitations on the possible growth response to CO_2 are considered. The estimated rate of accumulation of carbon by the forest studied here is markedly greater than that, about 13 mol C m^{-2} a^{-1} (Fig. 9). This suggests that some other factor apart from "CO_2 fertilisation" must clearly be involved.

The importance of disturbance, particularly fire history, on the long- and short-term net ecosystem productivity of Siberian pine forests in the Zotino region has been emphasised by Wirth et al. (2002a). Their stand-specific estimate of the rate of net phytomass carbon accumulation, which takes into account the unusually long period that the study stand has not experienced any large-scale ground fires was, however, only about 2.5 mol C m^{-2} a^{-1} with almost all of this above ground. That analysis, however, only considered the soil organic layer, and provided only a long-term estimate of the rate of carbon accumulation by that layer (0.1 mol C m^{-2} a^{-1}) from a chronosequence approach. However, as is evident in Fig. 9, if we are to accept the validity of the eddy covariance N_E estimate of -13 mol C m^{-2} a^{-1}, then a quite massive accumulation of carbon (*ca.* 10 mol C m^{-2} a^{-1}) in the above-ground litter and soil carbon pools must have be occurring during the study period. As the above CWD litter pool has been estimated at less than 20 mol C m^{-2} a^{-1} (Wirth et al., 2002b), this inferred accumulation of carbon must be in the soil organic layer or the mineral soil. Measuring to 0.3 m depth, Wirth et al. (2002b) obtained a soil carbon density of 313 mol C m^{-2} a^{-1} and allowing for this to constitute 0.78 of the soil C to a depth of 1 m (Bird et al., 2002) this gives a soil C content to 1 m depth for the study stand of about 400 mol C m^{-2}. Over the long-term the rate of accumulation implied by Fig. 9 therefore requires that the soil C pool should double within the next 40 yr. This is extremely unlikely given the limited ability of sandy soils in the region to store significant amounts of carbon (Bird et al., 2002). It is also unlikely that large amounts of carbon could be leaving the forest through leaching losses. Based on soil water dissolved organic carbon concentrations and drainage estimates, Gleixner and Lloyd (personal communication) have estimated that these losses should amount to 1.5 mol C m^{-2} a^{-1} at most. It is, however, worth pointing out the relatively low heterotrophic respiration rate implied in the current study (Fig. 9) is itself consistent with the conclusion of Šantrůčková et al. (2002) who, working in the same area, found that the coarse textured Zotino soil had a low mineralisation potential. They also found a substantial part of the C consumed in heterotrophic metabolism to be built into microbial products and transformed to soil organic carbon rather than mineralised.

As has been discussed above, we have as much confidence in our eddy covariance measurements as is possible given current knowledge, and all known required corrections have been made; including an allowance for some "flux loss" under conditions of low night-time turbulence. It therefore seems likely that if the implied accumulation of 10 mol C m^{-2} a^{-1} in the soil carbon pool is real, then it can only be so in the short term. Two possibilities emerge to explain this. Firstly 1999 and 2000 may have been years of unusually high G_P or, alternatively, heterotrophic respiration rates may have been substantially lower than the long-term norm. We do not have sufficient long-term data to check these possibilities at this stage, though we do point out that adverse effects of soil water deficit on soil respiration rates were observed in 1999 by Shibistova et al. (2002a) and in a nearby forest for 1996 by Kelliher et al. (1999). Of the intervening years, 1998 was also unusually dry (Tchebakova et al., 2002), this appearing to be a longer-term trend (Arneth et al., 2002). It may then be that some sort of debilitation of the soil microbial populations in response to soil water deficit had been occurring over some years prior to 2000. Our own observations for 2001 with soil chamber respiration measurements, a second moist year after 2000, suggest nearly two-fold higher soil respiration rates in that year than in either 1999 or 2000 (Shibistova and Santos; unpublished observations). However, any real support for the above speculation will require several further years of eddy covariance studies with complementary studies of biological and physical aspects of soil carbon dynamics in the study stand.

5. Acknowledgements

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REFERENCES

Arbarskaya, M. K. and Vaganov, E. A. 1997. Long-term variation in fire frequency and radial increment in pine from the middle taiga subzone of central Siberia. *Russ. J. Ecol.* **28**, 291–297.

Arneth, A., Lloyd, J., Šantrůčková, H., Bird, M. I., Grigoriev, S., Kalaschnikov, Y. N., Gleixner, G. and Schulze, E.-D. 2002. Response of central Siberian Scots pine to soil water deficit and long-term trends in atmospheric CO_2 concentration. *Global Biogeocheml. Cycles* (in press).

Baldocchi, D., Valentini, R., Oechel, W. and Dahlman, R. 1996. Strategies for measuring and modelling carbon dioxide and water vapour fluxes over terrestrial ecosystems. *Global Change Biol.* **2**, 159–168.

Baldocchi, D. D., Vogel, C. A. and Hall, B. 1997. Seasonal variation of carbon dioxide exchange rates above and below a boreal jack pine forest. *Agric. For. Meteorol.* **83**, 147–170.

Baldocchi, D., Falge E., Gu, L. H. and coauthors. 2001. FLUXNET: A new tool to study the temporal and spatial variability of ecosystem-scale carbon dioxide, water vapour and energy flux densities. *Bull. Am. Meteorol. Soc.* **82**, 2415–2434.

Bird, M., Šantrůčková, H., Arneth, A., Grigoriev, S., Gleixner, G., Kalashnikov, Y. N., Lloyd, J. and Schulze, E.-D. 2002. Soil carbon inventories and carbon-13 on a latitude transect in Siberia. *Tellus* **54B**, this issue.

Chen, J. M., Rich, P. M., Gower, S. T., Norman, J. M. and Plummer, S. 1997. Leaf area index of boreal forests: theory, techniques and measurements. *J. Geophys. Res.* **102**, 29429–29443.

Ciais, P., Peylin, P. and Bousquet, P. 2000. Regional biospheric carbon fluxes as inferred from atmospheric CO_2 measurements. *Ecol. Appl.* **10**, 1574–1589.

Cowan, I. R. 1977. Stomatal behavior and environment. *Adv. Bot. Res.* **4**, 117–228.

Dang, Q. L., Margolis, H. A., Sy, M., Coyea, M. R., Collatz, G. J. and Walthall, C. L. 1997. Profiles of photosynthetically active radiation, nitrogen and photosynthetic capacity in the boreal forest: Implications for scaling from leaf to canopy. *J. Geophys. Res.* **102**, 28845–28859.

Ericsson, A. 1979. Effects of fertilization and irrigation on seasonal changes in carbohydrate reserves in different age classes of needles on 20-year old Scots pine trees (*Pinus sylvestris*). *Physiol. Plant.* **45**, 270–280.

Eugster, W. and Senn, W. 1995. A cospectral correction model for measurements of turbulent NO_2 flux. *Boundary-Layer Meteorol.* **74**, 321–340.

Fan, S, Gloor, M., Mahlman, J., Pacala, S., Sarmiento, J., Takahashi, T. and Tans, P. 1998. A large terrestrial sink in North America implied by atmospheric and oceanic carbon dioxide data and models. *Science* **282**, 754–759.

Foken T. and Wichura, B. 1996. Tools for quality assessment of surface-based flux measurements. *Agric. For. Meteorol.* **78**, 83–105.

Garratt, J. R. 1992. *The atmospheric boundary layer.* Cambridge University Press, Cambridge.

Goulden, M. L., Munger J. W., Fan, S. M., Daube, B. C. and Wofsy, S. C. 1996. Exchange of carbon dioxide by a deciduous forest; Response to interannual climate variability. *Science* **271**, 1576–1578.

Goulden, M. L., Wofsy, S. C., Harden, J. W., Trumborne, S. E., Crill, P. M., Gower, S. T., Fries, T., Daube, B. C., Fan, S.-M., Sitton, D. J., Bazzaz, F. A. and Munger, D. W. 1998. Sensitivity of boreal forest carbon balance to soil thaw. *Science* **279**, 214–217.

Grace, J., Lloyd, J., Miranda, A. C., Miranda, H. and Gash, J. H. C. 1998. Fluxes of carbon dioxide and water vapour over a C_4 pasture in south-western Amazonia (Brazil). *Aust. J. Plant Physiol.* **25**, 519–530.

Hari, P., Mäkelä, A., Berninger, F. and Pohja, T. 1999. Field evidence for the optimality hypothesis of gas exchange in plants. *Aust. J. Plant Physiol.* **26**, 239–244.

Hollinger, D. Y., Kelliher, F. M., Schulze, E.-D., Bauer, G., Arneth, A., Byers, J. N., Hunt, J. E., McSeveny, T. M., Kobak, K. I., Milyukova, I., Sogachev, A., Tatarinov, F., Varlagin, A., Ziegler, W. and Vygodskaya, N. N. 1998. Forest–atmosphere carbon dioxide exchange in eastern Siberia. *Agric. For. Meteorol.* **90**, 291–306.

Janssens, I. A., Lankreijer, H., Matteucci, G. et al. 2001. Productivity overshadows temperature in determining soil and ecosystem respiration rates across European forests. *Global Change Biol.* **7**, 269–278.

Jarvis, P. G., Massheder, J. M., Hale, S. E., Moncreiff, J. B., Rayment, M. and Scott, S. L. 1997. Seasonal variation of carbon dioxide, water vapour and energy exchanges of a boreal black spruce forest. *J. Geophys. Res.* **102**, 28953–28966.

Kaminski, T., Heimann, M. and Giering, R. 1999. A coarse grid three-dimensional global inverse model of the atmospheric transport–2. Inversion of the transport of CO_2 in the 1980s. *J. Geophys. Res.* **104**, 18555–18581.

Kelliher, F. M., Lloyd, J., Arneth, A., Luhker, B., Byers, J. N., McSeveny, T. M., Milukova, I., Grigoriev, S., Panfyorov, M., Sogatcev, A., Varlagin, A., Ziegler, W., Bauer, G., Wong, S.-c. and Schulze, E.-D. 1999. Carbon dioxide efflux density from the floor of a central Siberian forest. *Agric. For. Meteorol.* **94**, 217–232.

Kelliher, F. M., Lloyd, J., Baldocchi, D. D., Rebmann, C., Wirth, C. and Schulze, E.-D. 2001. Evaporation in the boreal zone: Physics, vegetation and climate. In: *Global biogeochemical cycles in the climate system* (eds. E.-D. Schulze, S. P. Harrison, M. Heimann, E. A. Holland, J. Lloyd, I. C. Prentice and D. Schimel). Academic Press, New York,151–175.

Kossmann, J. and Lloyd, J. 2000. Understanding and influencing starch biochemistry. *Crit. Rev. Plant Sci.* **19**, 171–226.

Krivosheeva, A. Tai, D.-L., Ottander, C., Wingsle, G., Dube, S. K. and Öquist, G. 1996. Cold acclimation and photoinhibition of photosynthesis in Scots pine. *Planta* **200**, 296–305.

Lindroth, A., Grelle, A. and Morén, A.-S. 1998. Long-term measurements of boreal forest carbon balance reveal large temperature sensitivity. *Global Change Biol.* **4**, 443–450.

Lloyd, J. 1991. Modelling stomatal response of Macadamia integrifolia. *Austr. J. Plant Physiol.* **18**, 549–660.

Lloyd, J. 1999a. Current perspectives on the terrestrial carbon cycle. *Tellus* **51B**, 336–342.

Lloyd, J. 1999b. The CO_2 dependence of photosynthesis, plant growth responses to elevated CO_2 concentrations and their interactions with soil nutrient status II. Temperate and boreal forest productivity and the combined effects of increasing CO_2 concentrations and increased nitrogen deposition at a global scale. *Funct. Ecol.* **13**, 439–459.

Lloyd, J. and Farquhar, G. D. 1994. ^{13}C discrimination during photosynthetic CO_2 assimilation by the terrestrial biosphere. *Oecologia* **99**, 201–215.

Lloyd, J. and Farquhar, G. D. 1996. The CO_2 dependence of photosynthesis, plant growth responses to elevated atmospheric CO_2 concentrations and their interaction with plant nutrient status. *Funct. Ecol.* **10**, 4–32.

Lloyd, J. and Farquhar, G. D. 2000. Do slow-growing species and nutrient-stressed plants consistently respond less to elevated CO_2? A clarification of some issue raised by Poorter (1998). *Global Change Biol.* **6**, 871–876.

Lloyd, J., Grace, J., Miranda, A. C., Meir, P., Wong, S. C., Miranda, H. S., Wright, I. R., Gash, J. H. C. and McIntyre, J. 1995. A simple calibrated model of Amazon rainforest productivity based on leaf biochemical poperties. *Plant, Cell Environ.* **18**, 1129–1145.

Lloyd, J., Francey, R. J., Mollicone, D., Raupach, M. R., Sogachev, A., Arneth, A., Byers, J. N., Kelliher, F. M., Rebmann, C., Valentini, R., Wong, S.-C., Bauer, G. and Schulze, E.-D. 2001. Vertical profiles, boundary-layer budgets, and regional flux estimates for CO_2, and its $^{13}C/^{12}C$ ratio and for water vapor above a forest/bog mosaic in central Siberia. *Global Biogeochem. Cycles.* **15**, 267–284.

McMillen R. T. 1988. An eddy correlation technique with extended applicability to non-simple terrain. *Boundary-Layer Meteorol.* **43**, 231–245.

McNaughton, K. G. 1994. Effective stomatal and boundary layer resistance of heterogeneous surfaces. *Plant Cell Environ.* **17**, 1061–1068.

Makkonen, K. and Helmisaari, H.-S. Fine root biomass and production in Scots pine stands in relation to stand age. *Tree Physiol.* **21**, 193–198.

Malhi, Y., Baldocchi, D. D. and Jarvis, P. G. 1999. The carbon balance of tropical temperate and boreal forests. *Plant Cell Environ.* **22**, 715–740.

Milyukova, I. M., Kolle, O., Varlagin, A. B., Vygodskaya, N. N., Schulze, E.-D. and Lloyd, J. 2002. Carbon balance of a southern taiga spruce stand in European Russia. *Tellus* **54B**, this issue.

Nichol, C. J., Lloyd, J., Shibistova, O., Arneth, A., Röser, C., Knohl, A., Matsubara, S. and Grace, J. 2002. Remote sensing of photosynthetic light-use efficiency of Siberian boreal forest. *Tellus* **54B**, this issue.

Öquist, G., Brunes, L., Hällgren, J.-E., Gezelius, K., Hellén, M. and Malmbberg, G. 1980. Effects of artificial forest hardeining and winter stress on net photosynthesis, photosynthetic electron transport and RuBP carboxylase activity in seedlings on Pinus sylvestris. *Physiol. Plant.* **48**, 526–531.

Orr, J. C., Maier-Reimer, E., Mikolajewicz, U., Monfray, P., Sarmiento, J. L., Toggweiler, R. J., Taylor, N. J., Palmer, J., Gruber, N., Sabine, C. L., Le Quéré, C., Key, R. M. and Boutin, J. 2001. Estimates of anthropogenic carbon uptake from four 3-D global ocean models. *Global Biogeochem. Cycles* **15**, 43–60.

Ottander, C., Campbell, D. and Öquist, G. 1995. Seasonal changes in Photosystem II organisation and pigment composition in *Pinus sylvestris*. *Planta* **197**, 176–183.

Paul, M. J. and Foyer, Ch. H. 2001. Sink regulation of photosynthesis. *J. Exp. Bot.* **52**, 1383–1400.

Paulson, C. A. 1970. The mathematical representation of on windspeed and temperature profiles in the unstable surface layer. *J. Appl. Meteorol.* **9**, 857–861.

Prentice, I. C., Farquhar, G. D., Fasham, M., Goulden, M., Heimann, M., Jaramillo, V., Kheshgi, H., Le Quéré, C., Scholes, R. and Wallace, D. 2001. The carbon cycle and atmospheric CO_2. In: *Climate change: the scientific basis: The contribution of WGI of the IPCC to the IPCC Third Assessment Report (TAR)*. (eds. J. Houghton and D. Yihui). Cambridge University Press,183–237.

Rayner, P. J., Enting, I. G., Francey, R. J. and Langenfelds, R. 1999. Reconstructing the recent carbon cycle from atmospheric CO_2, ^{13}C and O_2/N_2 observations. *Tellus* **51B**, 213–232.

Ryan, M. G., Lavigne, L. B. and Gower, S. T. 1997. Annual carbon cost of autotrophic respiration in boreal forest ecosystems in relation to species and climate. *J. Geophys. Res.* **102**, 28871–28883.

Šantrůčková H., Bird, M. I., Kalashnikov, Y. N., Grund, M., Elhottova, D., Simek, M., Grigoryev, S., Gleixner, G., Arneth, A., Schulze, E.-D. and Lloyd, J. Microbial characteristics of soils on a latitudinal transect in Siberia. *Global Change Biol.* (in press).

Savitch, L. V., Leonardos, E. D., Krol, M., Jansson, S., Grodzinski, B., Huner, N. P. A. and Öquist, G. 2002. Two different strategies for light utilization in photosynthesis in relation to growth and cold acclimation. *Plant Cell Environ.* **25**, 761–771.

Sawamoto, T., Hatano, R., Yajima, R., Takahashi, K and Isaev, A. P. 2000. Soil respiration in Siberian taiga ecosystems with different histories of forest fire. *Soil Sci. Plant Nutr.* **46**, 31–42.

Schulze, E.-D., Lloyd J., Kelliher, F. M., Wirth, C., Rebmann, C., Lühker, B., Mund, M., Knohl, A., Milyukova, I. M., Schulze, W., Ziegler, W., Varlagin, A. B., Sogachev, A. F., Valentini, R., Dore, S., Grigoriev, S., Kolle, O., Panfyorov, M. I., Tchebakova, N. and Vygodskaya, N. N. 1999. Productivity of forests in the Eurosiberian boreal region and their potential to act as a carbon sink – a synthesis. *Global Change Biol.* **5**, 703–722.

Shibistova, O., Lloyd, J., Evgrafova, S., Savushkina, N., Zrazhewskaya, G., Arneth, A., Knohl, A., Kolle, O. and Schulze, E.-D. 2002a. Seasonal and spatial variability in soil CO_2 efflux rates for a central Siberian Pinus sylvestris forest. *Tellus* **54B**, this issue.

Shibistova, O., Lloyd, J., Zrazhewskaya, G., Arneth, A., Kolle, O., Astrakhantceva, N., Shijneva, I., Knohl, A. and Schmerler, J. 2002b. Ecosystem respiration budget for a Pinus sylvestris stand in central Siberia. *Tellus* **54B**, this issue.

Shibistova, O. B., Lloyd, J., Kolle, O., Arneth, A., Tchebakova, N. M., Zolotoukhine, D. A., Zrazhewskaya, G. and Schulze, E.-D. 2002c. Eddy covariance assessment of CO_2 accumulation by mature pine forest. *Dokl. Akad. Nauk* **383**, 1–5 (in Russian).

Sudachkova, N. E., Romanova, L. I., Milyutina, I. L., Kozhevnikova, N. N. and Semenova, G. P. 1994. Environmental stress impact on carbohydrate level and distribution in tissues of Scots pine in Siberia. *Lesovedenie* **6**, 3–9 (in Russian).

Tans, P. P., Fung, I. Y. and Takahashi, T. 1990. Observational constraints of the global atmospheric CO_2 budget. *Science* **247**, 1431–1438.

Tchebakova, N. M., Kolle, O., Zolotoukhin, D., Arneth, A., Styles, J. M., Vygodskaya N. N., Schulze, E.-D., Shibistova, O. and Lloyd, J. 2002. Inter-annual and seasonal variations of energy and water vapour fluxes above a Pinus sylvestris forest in the Siberian middle taiga. *Tellus* **54B**, this issue.

Valentini, R., Metteucci, G., Dolman, A. J. et al. 2000. Respiration as the main determinant of carbon balance in European forests. *Nature* **404**, 861–865.

Van der Werf, A., Poorter, H. and Lambers, H. 1994. Respiration as dependent on a species' inherent growth rate and on nitrogen supply to the plant. In: *A whole plant perspective on carbon–nitrogen interactions* (eds. J. Roy and E.Garnier), SPB Publishing, The Hague, 91–110.

Vogg, G., Helm, R., Hansen, J., Schäfer, C. and Beck, E. 1998. Frost hardening and photosynthetic performance of Scots pine (*Pinus sylvestris* L.) needles. I. Seasonal changes in the photosynthetic apparatus and its function. *Planta* **201**, 193–200.

Waring, R. H., Landsberg, J. J. and Willians, M. 1998. Net primary production of forests: a constant fraction of gross primary production? *Tree Physiol.* **18**, 135–140.

Wirth, C. 2000. *Der Einfluß von Feuer auf den Kohlenstoffhausalt sibirischer Kiefernwälder (Pinus sylvestris L.) unter biogeochemischen und populationsbiologischen Aspekten.* Ph.D. Thesis, University of Bayreuth, 260 pp.

Wirth, C., Schulze, E-.D., Schulze, W., von Stünzer-Karbe, W., Zeigler, W., Milyukova, I. M., Sogatchev, A, Varlagin, A. B., Panfyorov, M., Grigoriev, S., Kusnetova, V., Siry, M., Hardes, G., Zimmermann, R. and Vygodskoya, N. N. 1999. Above-ground biomass and structure of pristine Siberian Scots pine forests as controlled by competition and fire. *Oecol.* **121**, 66–80.

Wirth, C. Czimczik, C. I. and Schulze, E.-D. 2002a. Beyond annual budgets: carbon flux at different temporal scales in fire-prone Siberian Scots pine forests. *Tellus* **54B**, this issue.

Wirth, C., Schulze, E.-D., Kusznetova, V., Hardes, G., Siry, M., Schulze, B. and Vygodskaya, N. N. 2002b. Aboveground net primary productivity of Siberian Scots pine forest – Magnitude and causes of variability at different timescales. *Tree Physiology* **22**, 537–552.

Wirth, C., Schulze, E.-D., Lühker, B., Grogoriev, S., Siry, M., Hardes, G., Zeigler, W., Backor, M., Bauer, G. and Vygodskaya, N. N. 2002c. Fire and site type effects on the long-term carbon and nitrogen balance in pristine Siberian Scots pine forests. *Plant and Soil* (in press).