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Seasonal and spatial variability in soil CO_2 efflux rates for a central Siberian *Pinus sylvestris* forest

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ABSTRACT

Rates of CO_2 efflux from the floor of a central Siberian Scots pine (*Pinus sylvestris*) forest were measured using a dynamic closed chamber system and by a eddy covariance system placed 2.5 m above the forest floor. Measurements were undertaken for a full growing season: from early May to early October 1999. Spatial variability as determined by the chamber measurements showed the rate of CO_2 efflux to depend on location, with rates from relatively open areas ("glades") only being about 50% those observed below or around trees. This was despite generally higher temperatures in the glade during the day. A strong relationship between CO_2 efflux rate and root density was observed in early spring, suggesting that lower rates in open areas may have been attributable to fewer roots there. Continuous measurements with the eddy covariance system provided good temporal coverage. This method, however, provided estimates of ground CO_2 efflux rate rates that were about 50% lower than chamber measurements that were undertaken in areas considered to be representative of the forest as a whole. An examination of the seasonal pattern of soil CO_2 efflux rates suggests that much of the variability in CO_2 efflux rate could be accounted for by variations in soil temperature. Nevertheless, there were also some indications that the soil water deficits served to reduce soil CO_2 efflux rates during mid-summer. Overall the sensitivity of CO_2 efflux rate to temperature seems to be greater for this boreal ecosystem than has been the case for most other studies.

1. Introduction

The efflux of CO_2 from the soil surface is ultimately attributable to biological activity and must be approximately equal in magnitude to the sum of plant net primary production and root respiration (Lloyd and Farquhar, 1996). Current estimates of its global magnitude are of order 80 Gt yr^{-1} (Raich and Schlesinger, 1992).

Of this amount, the forests of Siberian Russia, which account for over 20% of the global forest area (Schulze et al., 1999), should constitute an appreciable proportion. Yet to date there has only been a limited amount of data available on soil efflux and its primary biotic and edaphic determinants for this large boreal region: short-term studies in a *Pinus sylvestris* stand by Kelliher et al. (1999) and Ross et al. (1999) near Zotino in Central Siberia (the area of the current study), in *Larix gmelinii* stands, also in Central Siberia (Yanagihara et al., 2000), and in *Larix cajanderi* stands near Yakutsk in Eastern Siberia (Sawamoto et al., 2000).

The studies of Ross et al. (1999) and Kelliher et al. (1999) suggested a more or less typical temperature dependence of soil CO_2 efflux rates on soil temperature for central Siberian pine forest. Kelliher et al. (1999) also emphasised the possible adverse effects of low

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levels of soil moisture on soil CO_2 efflux rates during dry summer periods. Overall, summertime soil CO_2 efflux rates were low compared to other boreal forests in Europe and North America, and this was attributed to low soil carbon contents of fire-prone forests growing on sandy soils rather than distinctive metabolic potentials of the soil microbial populations (Ross et al., 1999). Summertime respiration rates for the *Larix* stands were higher than those recorded for *P. sylvestris* in Central Siberia (Sawamoto et al., 2000; Yanagihara et al., 2000), with the study of Sawamoto et al. (2000) emphasizing the importance of fire history on soil CO_2 efflux rate.

All the above studies were, however, limited to field campaigns and did not ascertain the overall seasonal pattern of soil CO_2 efflux rates, and hence the full range its underlying controls. Here we report on both seasonal and spatial patterns of soil respiration measured underneath a stand of Scots pine (*Pinus sylvestris* L.) growing in Central Siberia. We studied the seasonal pattern of soil CO_2 efflux rates using both eddy covariance and chamber techniques, also examining seasonal changes in microbial population structure and sources of spatial variability in soil CO_2 efflux rates. Data from this study form the basis of an accompanying paper, in which estimates of the annual respiratory balance of the stand at the ecosystem level are given (Shibistova et al., 2002).

2. Materials and methods

2.1. Site description

The measurement site was located near the village of Zotino, about 30 km west of the Yenisei river at the eastern edge of the West Siberian Plain (60°44′N, 89°09′E). The eddy tower was established in a fire successional pine forest (*Pinus sylvestris* L.) with lichen understorey (Wirth et al., 1999; 2002a,b). The stand was 200 yr old, extending at least 0.5 km in all directions (Bird et al., 2002; Tchebakova et al., 2002). Stand structure was relatively homogeneous, with a stem density of around 470 ha^{-1}; basal area was 30 m^{-2} ha^{-1}; leaf area index (LAI) was 1.5 m^2 m^{-2}; and biomass (dry weight) was 10.7 kg m^{-2} (Wirth et al., 1999); In that paper the stand is designated as "200_{ld}", i.e. a 200 yr pine forest with lichen groundcover on a dry site.

As with most of the *P. sylvestris* forests in the area, the stand was located on gently undulating, alluvial sands with no underlying permafrost. The soils of the area are generally classified as Inceptisols. At the measurement site, based on the soil temperature, moisture regime, and nutrient status, the soil is characterised according to the US Classification System (Soil Survey Staff, 1999) as a Typic Dystrustept (C. Czimcik, personal communication). Generally the clay content in the mineral soil is <5%, and the soil was stone-free except for a few examples that were found at 1.25–1.50 m depth. In soil pits and auger holes within the vicinity of the tower a shallow layer of very densely packed sandy clay was repeatedly found between the depth of 1.50–2.00 m, with rusty spots in this lens indicating a fluctuating water table. Underneath this sandy clay layer coarse sands prevailed (C. Czimcik, personal communication).

Second to *Larix, P. sylvestris* is one of the most abundant Siberian tree species. It occupies about 14% of the Siberian forested area (Shvidenko and Nilsson, 1994). It is typically found on sandy soils. Over a large region from the Ural Mountains to the Yenisei River it often occurs in a mosaic, interspaced with extensive bog areas that tend to occur on lower ground. A description of the region in general is provided in Schulze et al. (2002).

2.2. Eddy covariance measurements

Eddy covariance measurements of carbon dioxide, water vapour, heat, and momentum fluxes were measured at a height of 2.5 m above the soil surface. 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, 10 cm below the sonic measurement height through BEV-A-Line tubing (15 m length and 1/4″ inner diameter) and two aerosol filters (ACRO 50 PTFE 1 μm pore-size, Gelman, Ann Arbor, MI, USA) at a flow rate of 5.8 L min^{-1} (pump unit: KNF Neuberger, Germany). Output from the sonic anemometer and infrared gas analyser were read at 20 Hz through RS-232 ports onto 386-class computers, and all data were stored for subsequent analysis. Pressure in the infrared gas analyser was about 10 mbar above ambient as measured by the internal pressure sensor of the infrared gas analyser, and was accounted for by the internal software.

The fluxes were calculated offline as simple covariances of 30 min high-frequency time series of vertical

wind velocity with temperature, CO_2 density, or water vapour density. The time lag between measurements of vertical wind velocity and scalar densities due to transport in the tube was estimated by cross-correlation between both time series to be equal to approximately 1.5 s for carbon dioxide. The data were corrected by shifting the time series by the estimated time lag.

Frequency losses due to damping in the tube and analyser response were corrected using the approach by Eugster and Senn (1995). The correction parameter was determined from the cospectral analysis of vertical wind, temperature, and carbon dioxide time series was determined on weekly blocks of data and was typically 0.25. Water vapour dilution corrections were made with internal software of the LiCor 6262, and corrections of differences of the air pressure in the sampling cell and in the atmosphere were calculated automatically with a built-in pressure transducer. Coordinate rotation was applied (McMillen, 1998)

2.3. Supporting meteorological measurements

The main measurement tower at the site was 27 m high and was equipped with instruments to measure air temperature (model HMP35D, Helsinki, Vaisala, Finland) and numerous other micrometeorological variables (Lloyd et al., 2002). Two soil temperature profiles with 0.05, 0.15, 0.50, and 1.00 m depths in an area characterised by a relatively high tree density were also measured, each with PT100 sensors at the end of 10 mm diameter rods. All meteorological data were collected every 10 s, and 10 min averages were stored on a datalogger (Dl 3000, DeltaT, Burwell, UK).

2.4. Soil chamber measurements

Total CO_2 from the forest floor was measured using a dynamic closed-chamber gas exchange system (LI-COR 6400, Lincoln, NE, USA). To re-equilibrate the soil system with the ambient conditions and to minimise any influence of mechanical disturbance of soil surface on diffusion rates, polychlorovinyl soil collars were inserted through the forest floor into the soil, projecting not less then 5 cm above the uppermost ground layer.

Three areas of the forest were identified for chamber CO_2 efflux measurements. One was an open area of around 225 m^2 (referred to hereafter as "glade"), for which the ground cover consisted of only lichen species. The second area chosen for study was beneath or around trees, with the understorey consisting mostly of lichen species (referred to hereafter as "lichen"). The third groundcover category, typically found in moister areas characterised by a lower microrelief, consisted of *Vaccinium* species as well as some lichen cover (referred to hereafter as "vaccinium").

The "glade" area was located approximately 20 m to the south of the eddy covariance system and the "lichen" and "vaccinium" areas, in close proximity to each other, were located approximately 70 m to the north-east of the eddy covariance system.

In each of the three areas, six to nine soil collars were inserted for subsequent measurements not less than 24 h before the first measurement cycle. Measurements were made on 14 separate days in 1999 from before the beginning of snowmelt in early May until after the first snowfall in October. Usually measurements were made approximately every 4 h over a period of 18–24 h. Different locations were selected for each daily cycle.

2.5. Snow CO_2 efflux measurements

In early May 1999, CO_2 efflux rates through the 0.8 m snow pack were measured. This was achieved using the same protocol as described above for snow-free soil, with the soil collars being gently hammered into the snow at least 24 h before measurement. Rigorous examination of changes in CO_2 concentration, especially an absence of any change in the CO_2 concentration within the measuring system when the collar/chamber interface was exposed to human breath, indicated that, when the collars were carefully inserted, such a system was leak-proof and therefore the data obtained were reliable in that respect. It was not, however, possible to obtain reliable measurements with this methodology after snowmelt had commenced.

2.6. Relationship between soil CO_2 efflux rates and soil carbon and root densities

In an area located approximately 1 km from the main measurement site, a separate investigation was undertaken in mid-May 1999, about 1 wk after the snowmelt had finished there. In this experiment, seven measurement sites were randomly chosen, and three soil collars installed at each site. On the subsequent three days, soil CO_2 efflux rates were determined for each instillation using the chamber technique (Section 2.4) and a 5 cm diameter, 20 cm length soil core then taken from within each soil CO_2 efflux measurement collar after the last measurement. These cores

were immediately separated into A, AE, E, EB, and B horizons, and subsequently removed to the laboratory for analysis.

In the laboratory, roots were first removed by means of a 100 μm sieve and their dry weight determined after drying at 80 °C until constant dry weight was achieved. The root-free soil portion was dried at 105 °C to constant dry weight, and soil carbon content subsequently determined using the Walkey–Black modified acid-dichromate digestion method (Nelson and Sommers, 1982).

2.7. Soil microbiological populations

In early spring (just after snowmelt: 13 May 2000), mid-summer (27 July 2000) and early winter (20/11/00), soil samples were taken in a "lichen" area for subsequent determination of microbial population densities. On three randomly chosen locations, 20 cm depth soil profiles were dug and three soil samples from each were taken by means of sterilized spatulas through the profile according to the soil profile (A, AE, E, EB, and B horizons). Samples from each horizon were transferred to sterilized containers and transported to the laboratory for subsequent analysis of soil microbial population structure and density according to the methods described in Zvyagintsev (1991).

Once in the laboratory, samples from the same soil horizons were bulked, passed through a 100 μm diameter sieve to remove most of the root material present, and carefully homogenized. Sub-samples (10 g) of air-dried soil were then placed in sterilised glass containers. For the summer samples 90 mL of sterile water were subsequently added. For the early – spring and winter samples a 10% glycerol suspension was used. After 20 min shaking with an agitator, samples were left for 10 min to allow sedimentation to occur, and 0.05 mL of supernatant was subsequently placed on a solid nutrition medium within Petri dishes and incubated under constant temperature conditions. "Spring" and "winter" samples were exposed to 4 °C for 28 d. For the "summer" samples exposure was at 27 °C for 7 d. All analyses were taken in three replications.

To determinate different groups of micro-organisms four different nutrient media were used: beef extract (for isolation of organic nitrogen utilizing micro-organisms), amyl ammonia (for organisms utilizing non-organic nitrogen sources), wort agar (for detection of fungi) and soil extract agar (for the cultivation of oligotrophic micro-organisms).

The number of microbial colonies was accounted visually and the amount of colony-forming units (CFU) per g of air-dried soil was estimated using the equation:

$$A = K P W / V$$

where A is the amount of colony-forming units, K is the colony number per Petri dish, P is the degree of soil suspension dilution (1:10, 1:100 and 1:1000), V is the volume of soil suspension, and W is the soil moisture.

Although separate incubations were undertaken for the various soil horizons sampled, data presented here are pooled for the entire 0–20 cm core.

2.8. Determination of ground-layer biomass

In August 2000, the time of maximum foliar development for higher plants and mosses in the ground-layer, five 1 m^2 quadrates were randomly placed in areas identified as being characteristic of the "glade", "lichen", and "vaccinium" plots described in Section 2.4. Needles and twigs were removed, and the above biomass partitioned into higher plants, lichen, and moss. Upon return to the laboratory, plant dry weights were determined after drying in an oven at 85 °C for 24 h.

3. Results

3.1. Soil CO_2 efflux patterns during and after snow melt

For the period 1–13 May 1999, Fig. 1 shows observed patterns of changes in air temperature (Fig. 1a), soil temperature at 50 mm depth (Fig. 1b), as well as the chamber measurements and the continuous ground eddy covariance data (Fig. 1c). This period represents the second snowmelt, the first of which was of limited duration about 3 wk earlier. Over the period covered in Fig. 1, snowmelt was rapid, with the average snow depth (mean of 10 determinations randomly placed around the measurement area) declining from about 0.8 m on day of year (doy) 121 to a virtually snow free forest by doy 132 (data not shown). Spatial variability in the rate of snowmelt was, however, quite high. For the chamber data in Fig. 1, with the exception of the first two data points which represent snow-covered areas (doy 121) other chamber measurements represent early melting snow-free "lichen" areas located under trees.

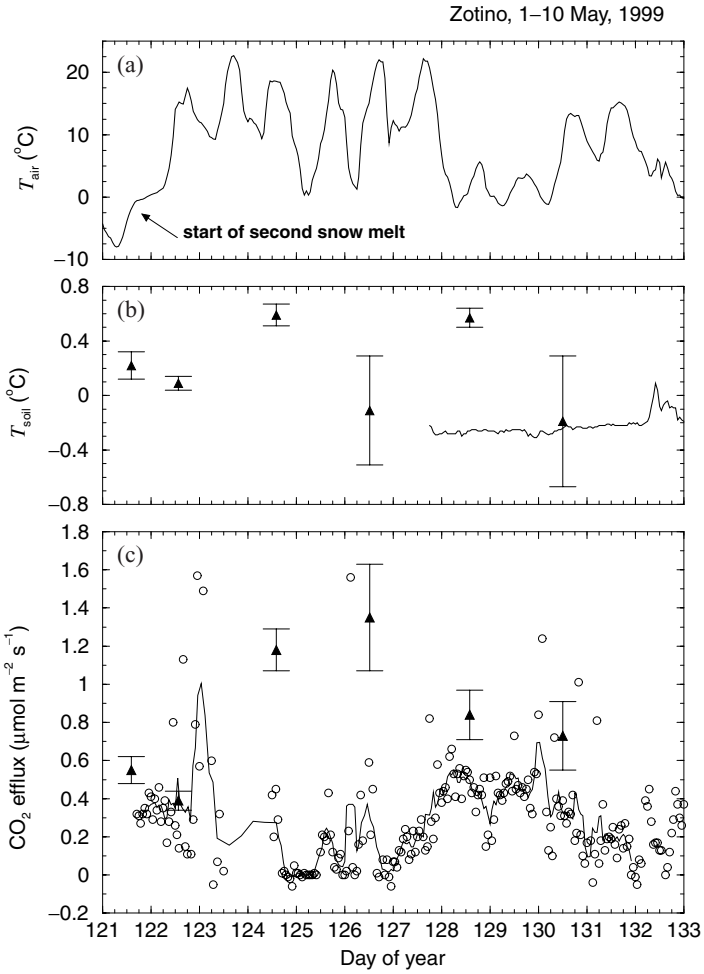

Fig. 1. Air and soil temperatures and ground CO_2 fluxes during snowmelt in Spring 1999: (a) air temperatures at 27 m; (b) ▲, soil temperatures at 10 cm depth as determined during the time of chamber CO_2 efflux measurement (±sd); solid line, 5 cm soil temperature as measured by the automatic weather station; (c) ▲, CO_2 efflux in the lichen area as measured by the chamber method (±sd); ○, 30 min average ground surface fluxes as measured by the ground level eddy covariance system; solid line, 3 h running mean of eddy covariance results.

From measurements made on the approximately 0.8 m deep snow pack on doy 121, snow CO_2 efflux rates of 0.15 to 0.25 μmol m^{-2} s^{-1} were observed. This is consistent with many recent observations showing a small but significant "winter respiration" of snow-covered soil. Thermal insulating properties of the snow cover are sufficient to maintain soil temperatures close to 0 °C and this allows some microbial activity to continue throughout the winter months (Zimov et al., 1993; Oechel et al., 1997; Winston et al., 1997; Mast et al., 1998; Grogan and Chapin, 1999). Although population levels are very low compared to those observed during summer, we have confirmed the presence of physiologically active micro-organisms in our soil during the winter period (Table 1).

Though significant, CO_2 efflux rates for snow-covered areas in early May were appreciably lower than those measured with the closed-chamber system on small patches of ground immediately after the snow had disappeared (0.6–1.4 μmol m^{-2} s^{-1}). This suggests large increases in soil efflux rates just after soil thaw. Similar elevated soil CO_2 efflux rates around the

Table 1. *Seasonal variation in fungal and bacterial population density in the top 20 cm of forest soil*

Date of sampling	Cell density ($\times 10^3$ cells gDW^{-1} soil) Fungi	Bacteria	Total
14 May 2000 (early spring)	237	70	307
27 July 2000 (mid-summer)	4493	5556	10049
28 November 2000 (early winter)	90	210	300

time of snowmelt have been observed before (Winston et al., 1997; Mast et al., 1998). It has been suggested that this "burst" of CO_2 emission from the soil may be attributable to increased respiratory activity by microorganisms due to enhanced substrate availability or nutrient supply as a consequence of the freeze/thaw process (Sommerfeld et al., 1991; Skogland et al., 1988; Brooks et al., 1997). This may similarly be the cause for the higher CO_2 efflux rates on recently exposed areas of the forest than for snow-covered areas discussed above, even though soil temperatures varied very little around this time, remaining at around 0 °C (Fig. 1). A significant increase in soil CO_2 efflux rates was also observed in the absence of any appreciable increase in soil temperature above 0 °C in the study of Mast et al. (1998).

No consistent pattern was observed in the ground eddy covariance measurements for the 12 d period after the second snow melt commenced, with the exception of markedly higher rates of soil CO_2 efflux on doy 123, just after the second snow melt had started (Fig. 1c). These higher fluxes persisted for nearly 24 hs, and we have no reason to suppose that they are a consequence of unusually high measurements errors during this period. Exposed (snow-free) area of the forest at this time was 1% at most, and thus the eddy covariance system would have been sampling almost entirely snow-covered areas (the average depth of snow on this day was 0.65 ± 0.04 m; $n = 10$). This burst, immediately after the commencement of snowmelt was of only 24 hs duration and is not readily attributable to the "freeze/thaw" mechanism for the recently exposed areas described above. More likely it is attributable to a simple physical process. One possibility is the rapid release of CO_2 accumulated within the snowpack, associated with the large increase in porosity that accompanies snowmelt, especially when ice layers are present (Colbeck and Anderson, 1982; Melloh and Crill, 1996; Albert and Perron, 2000).

For the ten days subsequent to Fig. 1, air and soil temperatures, incoming photosynthetically active radiation (PAR), and ground CO_2 fluxes as measured by eddy covariance are shown in Fig. 2. This shows a decline in air temperatures to doy 133, staying just above 0 °C until doy 135, after which they once again increased before a cooler period again occurring around doy 139. During the cooler periods, associated also with cloudy weather, incoming PAR was also typically lower (Fig. 2a). Soil temperatures stayed around 0 °C till doy 136 after which, associated with the warmer air temperatures, a gradual increase was observed, with a marked diurnal cycle in soil temperatures being apparent (Fig. 2b).

Although the ground-level CO_2 fluxes measured by the eddy covariance system were low, always less than 1 μmol m^{-2} s^{-1}, distinct diurnal trends were apparent. During the cooler periods (days 132–136) minimum fluxes were observed during the day, with a net uptake of CO_2 even being observed on doy 135. However, as soil temperatures increased, this phase was reversed; with maximum ground-level CO_2 fluxes being observed around solar noon. The one exception was doy 139 immediately after a rapid decline in air temperature.

Most likely, the above pattern was related to the physiological activity of the extensive lichen mat on the forest floor. Photosynthetic carbon uptake by lichen species requires high moisture availability (Palmqvist, 2000) and saturates at relatively low photon irradiances (Gauslaa and Sohlhaug, 1996). During the period during which low, or even negative, CO_2 efflux rates were observed from the forest floor, the ground was still very moist after the recent snow melt, and both air and soil temperatures were also low. As well as this period probably being characterised by low soil CO_2 efflux rates, low air temperatures probably assisted a positive net lichen C balance for the lichens present by virtue of lower respiration rates (Palmqvist, 2000)

3.2. Diurnal and seasonal patterns

Figure 3 shows a typical diurnal pattern obtained for soil chamber measurements in the "glade", "lichen", and "vaccinium" areas, as well as ground eddy covariance flux measurements and air and soil temperatures. On this cool summer day (26 June 1999), air temperatures varied between 8 and 14 °C, with soil temperatures depending strongly on location. Although in the "lichen" and "vaccinium" areas soil temperatures

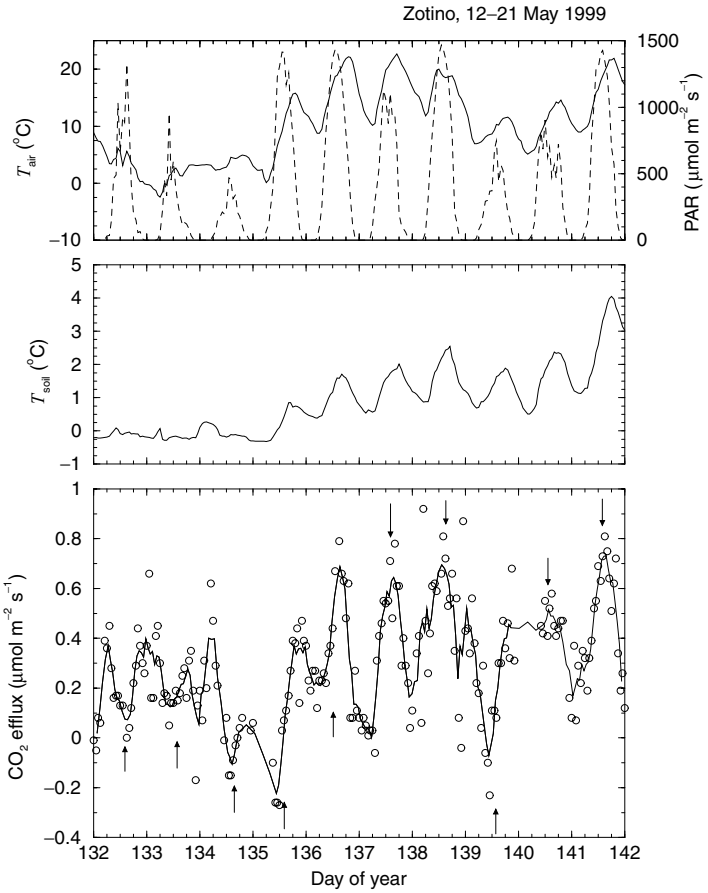

Fig. 2. Air and soil temperatures, photosynthetically active radiation (PAR) and ground CO_2 fluxes just after snowmelt in Spring 1999: (a) air temperatures at 27 m and PAR; (b) 5 cm soil temperature as measured by the automatic weather station; (c) ○, 30 min average ground surface fluxes as measured by the ground level eddy covariance system; solid line, 3 h running mean of eddy covariance results. To help the reader discern the contrasting diurnal patterns observed, arrows have been included for each day indicating the time of solar noon (ca. 1300 h local time).

varied little, between 7 and 9.5 °C (Fig. 3b) soil temperatures in the "glade" were much higher; being similar to or even greater than the air temperatures (Fig. 3a). Large effects of location were also observed in soil chamber CO_2 efflux rates, with rates from the "glade" substantially lower than in either the "lichen" or "vaccinium" areas. For the "vaccinium" plots, efflux rates were slightly higher than the "lichen" areas. In contrast to the efflux rates in the "glade", which followed the large diurnal soil temperature fluctuations in that area, little diurnal variation in soil CO_2 efflux rates was observed for the "vaccinium" or "lichen" plots. On this day the ground eddy covariance measurements showed a diurnal pattern similar in form and amount to the efflux rates observed in the "glade".

Figure 4a shows the seasonal patterns in the soil CO_2 efflux rates as measured by the eddy covariance system, as well as by the chamber method. Daily average soil temperatures at are shown in Fig. 4b, along with those observed for the chamber measurements (10 cm depth) in "lichen"/"vaccinium" areas and "glade". This shows the lower rates in the "glade" compared to the "lichen" and "vaccinium" areas as shown in Fig. 3 to be consistent throughout the year. This was despite typically higher temperatures in the open "glade", especially during summer. Similarly, the soil CO_2 efflux rates measured by the ground eddy system

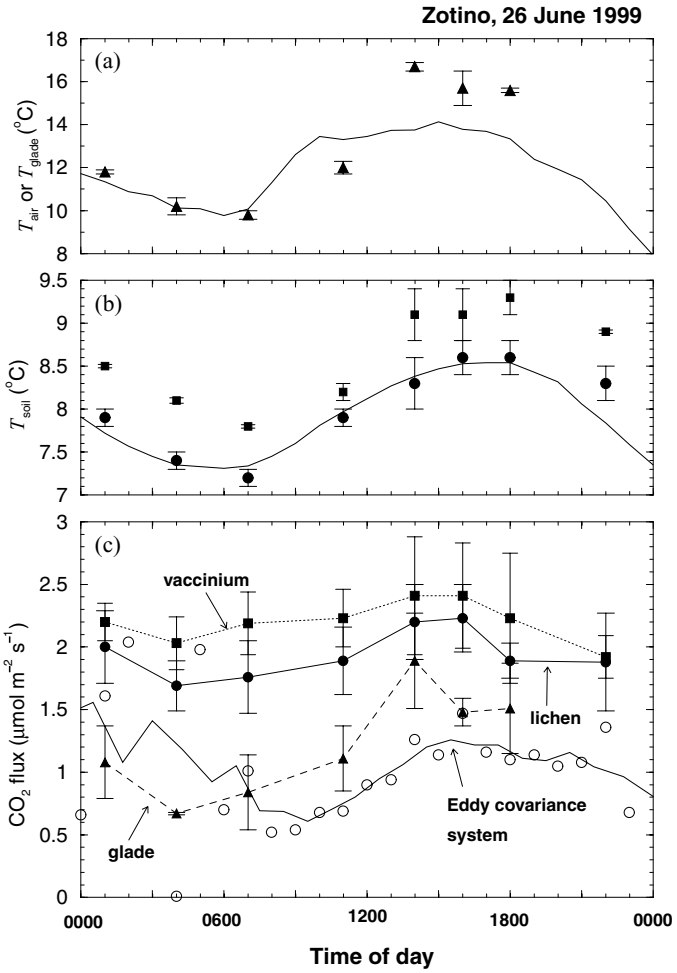

Fig. 3. Air and soil temperatures and ground CO_2 fluxes for 26 June 1999: (a) solid line, air temperatures at 27 m; ▲, soil temperatures at 0–10 cm depth in the "glade" as determined during the time of chamber CO_2 efflux measurement (±sd); (b) solid line, 5 cm soil temperature as measured by the automatic weather station; ●, soil temperatures at 0–10 cm depth in the lichen area as determined during the time of chamber CO_2 efflux measurement (±sd); ■, soil temperatures at 0–10 cm depth in the "vaccinium" area as determined during the time of chamber CO_2 efflux measurement (±sd); (c) ○, 30 min average ground surface fluxes as measured by the ground level eddy covariance system; solid line, 3 h running mean of eddy covariance results; ▲, soil CO_2 efflux rate in the "glade" area (±sd); ●, soil CO_2 efflux rate in the lichen area (±sd); ■, soil CO_2 efflux rate in the vaccinium area (±sd).

were usually lower than the "lichen"/"vaccinium" chamber measurements but of similar magnitude to the "glade" area.

Generally speaking, the seasonal pattern of ground efflux, especially as measured by eddy covariance system, reflected that of the soil temperatures as measured at 5 and 15 cm depth (Fig. 4b). Rates rose rapidly with the quickly increasing soil temperatures in June, generally fluctuated in phase with changes in soil temperature during July and August and then declined rapidly in September as the soil cooled. The relationship between soil efflux density and soil temperatures is considered further in Section 3.5.

3.3. Spatial variability

From Fig. 4, when measurements were made both in the open and covered areas of the forest, soil CO_2

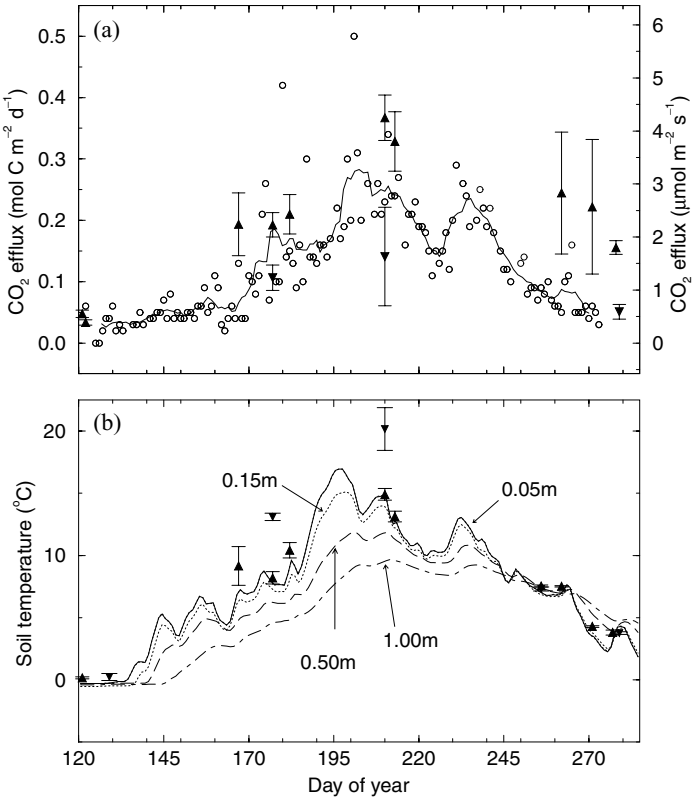

Fig. 4. The seasonal variation in soil CO_2 efflux rate and soil temperatures (a) ▲, mean measured soil CO_2 efflux rate in "lichen" and "vaccinium" areas as determined by chamber measurements (±sd); ▼, mean measured soil CO_2 efflux rate in "glade" area as determined by chamber measurements (±sd); ○, daily average ground surface fluxes as measured by the ground level eddy covariance system; solid line, 5 d running mean of eddy covariance flux: (b) daily average soil temperatures measured by the weather station: (———) 0.05 m; (· · · · · ·) 0.15 m; (– – – – –) 0.50 m; (— — — –) 1.00 m; ▲, mean measured soil temperatures during CO_2 efflux rate measurements in "lichen" and "vaccinium" areas (±sd); ▼, mean measured soil temperatures during CO_2 efflux rate measurements in the "glade" (±sd).

efflux rates were about double in the areas in close proximity to trees as compared the open "glade" area. A large degree of spatial variability in soil CO_2 efflux rates has been observed before for both temperate (Law et al., 1999) and boreal (Rayment and Jarvis, 2000) coniferous forests. In that latter study for a relatively moist black spruce forest in Canada, variations in soil CO_2 efflux rates were correlated with the thickness of the dead moss layer. The situation for the forest studied here is somewhat different. Growing on a well drained sandy soil the ground layer is typically much drier. Thus more desiccation tolerant lichen species tend to prevail. However, variations in lichen density (live or dead) are unlikely to have been the source of the spatial variation in soil CO_2 efflux rates observed in the darkened soil respiration chamber. Indeed, when determined in August 2000, the density of lichens in the "glade" area with the lowest soil CO_2 efflux rate was 76 ± 6 gDW m^{-2}, substantially greater than in either the "lichen" or "vaccinium" areas (42 ± 13 and 18 ± 18 gDW m^{-2}, respectively). More likely for the forest here, the spatial variability was a consequence of the different plant communities present in the different areas.

The "glade" area studied probably represents a small-scale "lichen desert", where recurring fires have allowed the establishment of dominant lichen communities at the expense of other plant species (Kershaw, 1977; Schulze et al., 1999). With the exclusion of some isolated regenerating pine seedlings, this area

was characterized by a total absence of higher plants, an almost total absence of leaf litter. It also had less pronounced soil organic horizons than either the "lichen" or "vaccinium" areas (data not shown). All these three factors may have contributed to the lower soil CO_2 efflux rates there.

The slightly higher rates of CO_2 fluxes in the "vaccinium" as compared to the "lichen" area was not, however, readily associable with differences in above-ground higher plant or moss biomass. The total biomass of higher plants when measured in 2000 was 138 ± 10 and 121 ± 61 g DW m^{-2} for the "lichen" and "vaccinium" areas, respectively. Likewise for mosses, no large differences were apparent, equivalent values being 119 ± 14 and 84 ± 11 g DW m^{-2}. The relatively high density of higher plants in the "lichen" areas is attributable to the occasional presence of both *Dicranum bergeri* and *Pleurozium schreberi* there.

As well as the easily visible differences in above ground characteristics, a lower density of roots in the open "glade" area as compared to the "lichen" or "vaccinium" areas may also have contributed to the lower soil CO_2 efflux rates there. This can be seen in Fig. 5, which examines soil CO_2 efflux rate as a function of root density for measurements for an a nearby forested area in early spring. This shows a strong correlation between these two parameters, suggesting that variations in root density may be one cause for the spatial variability in soil CO_2 efflux rates observed in the main experiment. For the same sample plots that show the correlation in Fig. 5 there was no significant relationship between soil carbon density and soil CO_2 efflux rate (data not shown).

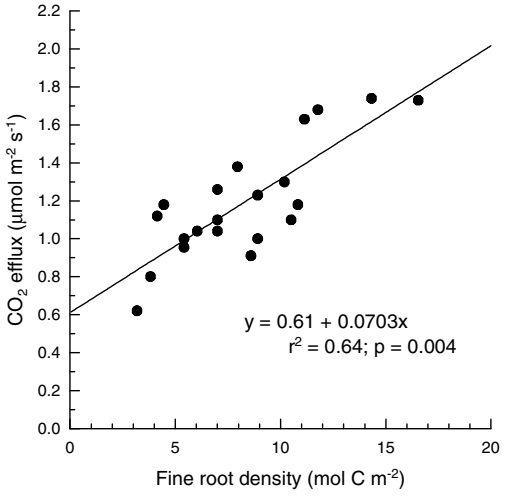

Fig. 5. The relationship between root density in the top 20 cm of soil and CO_2 efflux rate in early spring 1999. Data have been converted from a dry weight to a carbon basis using the value of 0.481 gC g^{-1} DW for fine roots obtained by Wirth et al. (2002a) in a nearby stand.

There are considerable uncertainties associated with an accurate estimation of the relative contributions of autotrophic versus heterotrophic respiration to the overall soil CO_2 flux (Buchmann, 2000; Hanson et al., 2000). However, it is well recognised that root respiration should be one of the major factors influencing the rate of soil CO_2 production in most ecosystems (Helal and Sauerbeck, 1991; Thierron and Laudelout, 1996). From a girdling experiment with *P. sylvestris* in northern Sweden it has been estimated that roots contributed about 55% of the total soil respiratory flux (Högberg et al., 2001). Figure 5 indicates that the proportion of ground CO_2 efflux attributable to roots is close to 0 in areas of the lowest root density, but might be as great as 0.8 in the areas of the highest root density.

3.4. Methodological differences

Although the soil CO_2 efflux rates from eddy covariance measurements were intermediate between the chamber measurements for "lichen" and "vaccinium" plots compared with the "glade", the tree distribution within the forest studied was only slightly non-random (Wirth et al., 1999). Relatively large open spaces such as the "glade" area examined here probably occupied less than 10% of the total forest area. On this basis then, both the "lichen" and "vaccinium" chamber measurements should have given similar rates to the eddy covariance measurements if there was not some systematic methodological bias. One problem might have been that the eddy covariance system was systematically sampling a "glade"-type area of the forest with an unusually low soil CO_2 efflux rate. However, this system was located in what was considered a typically dense area of the forest, where this ground vegetation type dominated. Using the model of Baldocchi (1997) we estimate a 90% footprint range for the eddy covariance system of less than 100 m under typical atmospheric conditions. It is therefore unlikely that unrepresentative sampling by the eddy covariance system was the cause of the discrepancies in Figs. 3 and 4.

There are, however, several other explanations for the discrepancy. Firstly, CO_2 exchange at a forest floor includes any photosynthetic and respiratory exchange

by the higher plants, moss, and lichen present, as well as the soil CO_2 efflux. This should cause differences between eddy covariance and chamber measurements during the day, especially in cases such at that here, where a non-transparent measurement chamber was used.

One means to assess the likely photosynthetic activity of the forest floor vegetation is to compare daytime versus night-time fluxes. For example, working in a boreal forest in Sweden and using transparent soil chambers, Moren and Lindroth (2000), found about a 20% reduction of daily soil CO_2 efflux rates which they attributed to daytime photosynthesis uptake by the relatively dense forest floor vegetation. Likewise, assuming daily respiration rates comparable to the night-time fluxes measured by eddy covariance in a spruce/pine stand with dense soil vegetation (shrubs seedlings and mosses covered most part of the forest floor), Constantin et al. (1999) estimated that soil CO_2 efflux rates were about 50% greater than the rate of understorey photosynthetic assimilation during the day.

For the forest studied here the situation would have been somewhat different to the above studies. There was only a low density of mosses and higher plants, which probably occupied less than 5% of the forest floor in total. However, ground cover of the C*ladina* and C*ladonia* species was close to 100%, and thus any net photosynthetic activity of these lichens could potentially account for the differences in the darkened soil chamber measurements and the ground eddy covariance system. From Fig. 2 it is clear that on some occasions net photosynthetic activity by the lichen layer was discernable, this being most prevalent on cooler days when the soil was moist. Similar diurnal patterns were also observed at other times of the year, typically occurring after significant rainfall events and when soil and air temperatures were low (data not shown). Nevertheless, implied rates observed were always low (less than 0.5 μmol m^{-2} s^{-1}) and limited to only a few days after rainfall.

The small magnitude of understorey photosynthetic activity on soil CO_2 efflux rates is shown in Fig. 6, which also emphasises the effect of methodology and location on the measured soil CO_2 efflux rate. Here chamber soil CO_2 efflux rates for "lichen"/"vaccinium" (combined) and "glade" areas

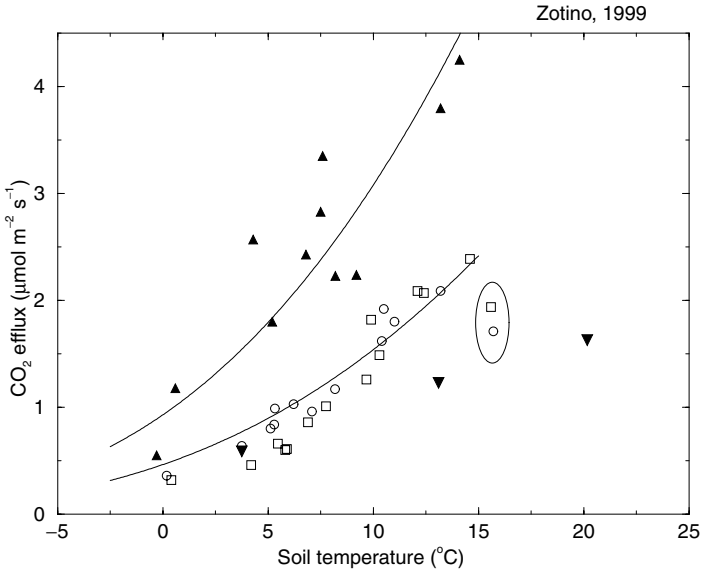

Fig. 6. The relationship between soil temperature and soil CO_2 efflux rate for measurements by the eddy covariance system and soil chamber. For the chamber measurements each value represents the daily mean average for measurements in the (▲) "lichen" and/or "vaccinium" areas or (▼) the open "glade" area. For the eddy covariance measurements, each point is the 10 d averages for (○) daytime and (□) night-time measurements. The two circled values represent eddy covariance measurements where effects of soil water deficit in reducing soil CO_2 efflux rates seems likely (Fig. 7; Section 3.5). They have not been included in the fitting of the model of Lloyd and Taylor (1994) to the daytime eddy covariance data (solid line). The fit of the Lloyd and Taylor (1994) model is also shown for the "lichen" and/or "vaccinium" chamber measurements.

are plotted as a function of soil temperature, along with measurements from the eddy covariance system; the latter being separated into night and day measurements: each point representing a 10 d average. At soil temperatures between 5 and 10 °C there are some indications of slightly lower soil CO_2 efflux rates during the day. This is consistent with the maximum photosynthetic activity of lichens under these conditions discussed above. However, overall, especially for the higher rates during summer there is little indication that photosynthetic activity by the ground layer during the day was responsible for the consistent differences between the eddy covariance system and the soil chamber measurements. Also shown in Fig. 6 are curves fitted to the "lichen"/"vaccinium" chamber and daytime ground eddy covariance measurements according to the model of Lloyd and Taylor (1994). Although giving a reasonable fit, the model seems to underestimate the magnitude of the temperature sensitivity of soil CO_2 efflux rates for both the chamber and eddy covariance system. The circled points were probably affected by low soil moisture status in mid-summer. The inter-relationships between soil temperature and soil moisture in determining overall rates of soil CO_2 efflux are discussed further in Section 3.5. This lack of a fit of the model of Lloyd and Taylor (1994) is considered in much more detail in an accompanying paper with alternative formulations for describing the temperature dependence of soil respiration for this ecosystem also being given (Shibistova et al., 2002).

A second possibility for the differences between the chamber and eddy covariance measurements might be that the eddy covariance system was systematically understimating fluxes due to suppressed or intermittent turbulence characteristics close to the forest floor (Janssens et al., 2001). Nevertheless, as was found by Kelliher et al. (1999) working a nearby *P. sylvestris* stand, cospectral analysis of turbulent fluctuations in vertical wind speed, w' and air temperature, T_a, showed the theoretical slope of $-4/3$ in the inertial subrange, the domain of energy cacsade whereby turbulent energy is transferred from lower to higher frequencies. Moreover, co-spectra for both the sonic anemometer and IRGA sensors showed a $-2/3$ slope in the inertial subrange (data not shown). This suggests that the eddy covariance system was obtaining high quality data. Analysis of co-spectra showed some loss of CO_2 flux, probably due to sensor separation and the dampening of CO_2 fluctuations in the closed system used here. Nevertheless, this has been corrected for here (Section 2.2). Thus, as has been argued by other authors (Constantin et al., 1999; Kelliher et al., 1999; Baldocchi, 2000), there is no reason to believe that if the appropriate corrections are made, that within forest measurements of fluxes using the eddy covariance technique should be in error. This is especially the case for the forest studied here which was relatively open, having a tree density of only 480 ha^{-1} and an LAI of 1.5 on a projected area basis (Wirth et al., 1999).

Even when eddy covariance measurements are made above a canopy, there are sometimes indications that some "loss of flux" may occur for under conditions of low wind speeds at night (Goulden et al., 1996; Jarvis et al., 1997). We have examined this problem closely elsewhere (Shibistova et al., 2002) and conclude that, in contrast to the eddy covariance system installed above the forest, flux "losses" at low turbulence were not a problem for the ground eddy covariance system in this experiment.

It is, however, well known that different soil CO_2 efflux measurement methodologies or even instruments can give vastly different soil CO_2 efflux estimates (Healy et al., 1996; Norman et al., 1997; Arneth et al., 1998; Le Dantec et al., 1999; Janssens et al., 2001), and the basis of these differences is not always well known or even consistent. For example, Norman et al. (1997) observed similar soil CO_2 efflux rate estimates for an eddy covariance system and dynamic closed-chamber system for one day but not another. It has been argued that closed chamber systems may underestimate soil CO_2 efflux because conventional calculations ignore the volume of air-filled spaces in the soil (Rayment, 2000). A counterbalancing effect is the likelihood of enhanced diffusion of CO_2 from the soil during the chamber measurements. This is thought to arise as a consequence of greater air movement within the closed-chamber system. However, it is not considered to be as great a problem for the LICOR-6000-09 chamber system used here as for some other dynamic closed systems (Le Dantec et al., 1999).

Law et al. (1999) have discussed the relative merits of chamber measurements versus ground level eddy covariance measurements. They point out, as is the case here, that chamber measurements allow the for the spatial variability in soil CO_2 efflux rates to be evaluated (Figs. 3 and 4) but the temporal variability of ground level fluxes can be better determined with high-frequency via the eddy covariance system (Fig. 3). For example, from the high-frequency eddy covariance data of Fig. 2 it can be concluded that some daytime uptake of CO_2 by understorey lichen vegetation

can occur almost immediately after snowmelt. It is unlikely that such a subtle response would be detectable using repeated chamber measurements.

3.5. *Effects of soil temperature and moisture status on soil CO_2 efflux rates*

Although from Fig. 6 it might be concluded that both chamber and eddy covariance measurements indicate that most of the seasonal variations in soil CO_2 efflux rates are attributable to variations in soil temperature, a closer examination of eddy covariance data show that this is not always the case. An example is shown in Fig. 7, where daytime average soil CO_2 efflux rates are plotted for the period doy 184 to doy 211 (2 July to 31 July). This represents a relatively hot and dry period where the only rainfall that occurred was 56 mm between days 199–201 (16–18 July). Although soil CO_2 efflux rates increased steadily with soil temperatures before the major rainfall, not only was there a substantially enhanced efflux of CO_2 of about 24 h duration associated with the cessation of the dry period, but also soil CO_2 efflux rates on subsequent days were significantly higher than before. This was despite lower soil temperatures.

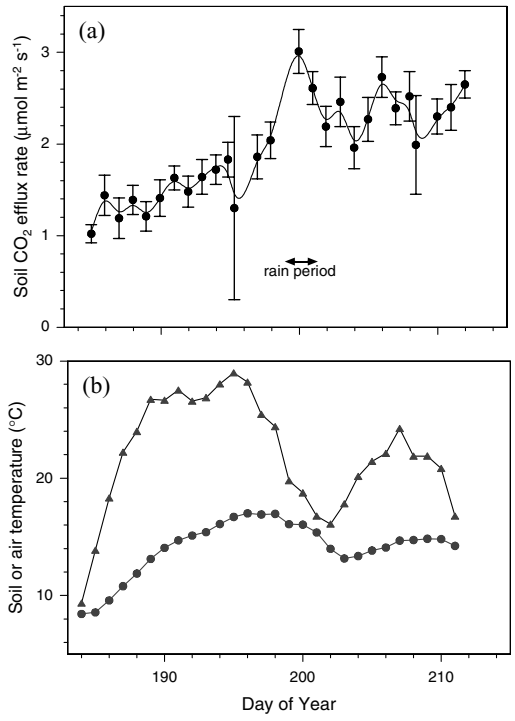

Fig. 7. Effect of rainfall on soil CO_2 efflux rates during summer. (a) Daily average CO_2 efflux rate (±standard error) as measured by the eddy covariance system from doy 184 to doy 211. (b) ●, daily average soil temperature at 0.05 m depth and ▲, daily average air temperature as measured above the forest for the same period.

A greatly enhanced efflux of CO_2 immediately after rain was also observed by Kelliher et al. (1999) working in a nearby forest in the summer of 1996. They attributed this effect to a rapid commencement of previously inhibited soil microbiological activity upon rewetting of the soil (Orchard and Cook, 1983). As well as this, it is also possible that respiratory activity of the lichen mat was involved. Upon rehydration of previously dry lichens, a burst of respiration can occur. This "resaturation respiration" is thought to almost certainly originate within the fungus and to reflect the initiation of repair mechanisms, particularly repair of drought damaged membranes (Brown et al., 1983; Palmqvist, 2000). Nevertheless, if any subsequent photosynthetic activity by the lichens were to have occurred, it must have been overridden by the generally higher soil CO_2 efflux rates after rain (Fig. 7), as daytime soil CO_2 efflux rates remained substantially higher than before the rain event. Effects of soil moisture on soil CO_2 efflux rates have also been reported for boreal forests in Alaska (Gulledge and Schimel, 2000) but as was also observed in that study, soil temperature is often the dominant factor modulating soil CO_2 efflux rates.

With the exclusion of the two "drought affected" points, this is also clear for the forest studied here (Fig. 6). Nevertheless, as is discussed elsewhere (Shibistova et al., 2002) the non-moisture-limited soil CO_2 efflux rates for this forest seem to be more strongly dependent upon soil temperature (Fig. 6) than is the case for a wide variety of ecosystems (Lloyd and Taylor, 1994). This also seems to be the case for the upland boreal forests in Alaska studied by Gulledge and Schimel (2000). This is somewhat surprising, as microbial incubation experiments using a soil obtained from a forest similar to the that studied here did not indicate an unusually high temperature sensitivity over the range 5–25 °C (Kelliher et al., 1999; Ross et al., 1999).

One possibility to account for this is the dramatic increase in soil microbial population density that occurs in this forest between early spring and summer (Table 1). A similar (though less dramatic) summer maximum in microbial biomass has been reported for a boreal forest soil in Alaska (Cochran et al., 1989).

This strong covariance of microbial activity and soil temperature, not generally discernable for more temperate forests (Wardle, 1998) might result in greater temperature sensitivity for soil CO_2 efflux rates for boreal and other high-latitude ecosystems than is the case for many other ecosystem types.

A second factor that may also be important in accounting for the strong seasonal pattern in CO_2 efflux rates changes observed are changes in the amount and physiological activity of roots during the growing season. There is clear evidence for a strong dependence on temperature for the rate of new root production in Scots pine (Domish et al., 2001), and working with Scots pine in eastern Siberia, Prokushkin (1982) observed the seasonal dynamics of root growth to depend mainly on air and soil temperatures, soil temperatures greater than about 5 °C being required for intensive root growth. He also observed that the physiological activity of roots was greatest during the maximum growth rate period. Bobkova (1987) reported a strong dependence of Scots pine root respiration rates on soil temperatures. Given the strong relationship between root density and CO_2 efflux rates, at least in early spring (Fig. 5), there may also be a strong covariance between intrinsic root physiological activity and soil temperatures for this ecosystem. Along with the large increase in microbial population density during the early growing season (Table 1), this may possibly also contribute to the strong temperature dependence of soil CO_2 efflux rates observed in the current study.

4. Conclusions

Eddy covariance measurements allowed for a good description of the temporal pattern in soil CO_2 efflux rates, whereas the chamber measurements allowed the spatial variability within the forest to be determined. Considerable spatial variability was observed, and this may have been related to variations in root density. Chamber CO_2 efflux rate measurements were, however, significantly higher than those measured by the eddy covariance system. Net assimilatory activity by the ground layer within this forest was minimal and unlikely to be responsible for the differences observed between the two measurement systems.

The seasonal pattern of CO_2 efflux rates was mostly accountable for by changes in soil temperature, but there were also indications that soil water deficits reduced CO_2 efflux rates during mid-summer. The temperature dependence of soil respiration appeared to be unusually high. This may have been a consequence of covariations between soil temperature and intrinsic microbiological and root activity during the short growing season.

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