PERGAMON

Soil Biology & Biochemistry 34 (2002) 1633–1646

Soil Biology & Biochemistry

www.elsevier.com/locate/soilbio

Climatic and resource quality controls on soil respiration across a forest–tundra ecotone in Swedish Lapland

Sofie Sjögersten*, Philip A. Wookey

Department of Earth Sciences, University of Uppsala, Villavägen 16, S-752 36 Uppsala, Sweden

Received 24 October 2001; received in revised form 10 June 2002; accepted 14 June 2002

Abstract

We studied resource quality and climatic constraints on soil respiration over a mountain birch forest–tundra ecotone in northern Swedish Lapland during 1999–2001 by means of both a field-based soil transplant experiment and a laboratory incubation experiment. Average carbon dioxide fluxes over the 2000 thaw season were 0.62 and 0.48 g CO_2 m^{-2} h^{-1}, at forest and tundra control plots, respectively. We attribute the higher respiration rate at the forest site mainly to more favourable microclimate but also to higher resource quality. Temperature–respiration relationships described using Arrhenius equations explained 37% of the variation in the tundra soil respiration and 42% for the forest soils on a season-wide basis in 2000. Q_{10} values (exponential temperature-response) were generally high (except in August in the field experiment) compared to the global average (2.4) and varied over time, with increased temperature-dependency at low soil temperatures. In the laboratory, higher activation energy was found in soils incubated at higher temperatures (12 and 17 °C; in the range 133–109 kJ mol^{-1}) compared with lower temperatures (2 and 7 °C; in the range 98–92 kJ mol^{-1}) suggesting an adaptation of the decomposer community toward more psychrophilic organisms or metabolism in low-temperature environments. Soil moisture, however, could also play an important role in modifying any temperature response of soil respiration in this sub-arctic ecotone area. These mesic soils have a relatively rapid turnover time of carbon and should be compared to boreal forest and temperate woodland in carbon dynamics. We conclude that a shift from tundra to birch forest would give an initial pulse of carbon released from soil to the atmosphere as labile carbon stored in tundra soils is metabolised by decomposer organisms.

Keywords: Arrhenius; Carbon dioxide; Ecotone; Soil respiration; Temperature

1. Introduction

Soil respiration is a major component of the global carbon cycle (Raich and Schlesinger, 1992; Schlesinger, 1997; Rustad et al., 2001) and is comparable in significance to net primary production (NPP) for the functioning of terrestrial ecosystems. Globally, soil respiration (R_s) releases between 50 and 70 Gt C yr^{-1} as CO_2 to the atmosphere (Raich and Schlesinger, 1992) and this flux is an order of magnitude higher than those resulting from direct anthropogenic activity (e.g. the burning of biomass and fossil fuels). In spite of the significance of R_s in the global C cycle there remains great controversy regarding the potential responses of respiration to changes in climate variables such as temperature, and to alterations in the quantity and quality of litter inputs (including roots and root exudates) and net primary productivity (Liski et al., 1999; Ågren, 2000; Buchmann, 2000; Giardina and Ryan, 2000; Fang and Moncrieff, 2001; Högberg et al., 2001; Janssens et al., 2001; Norby et al., 2001; Rustad et al., 2001).

Due to the integral involvement of R_s in the global carbon cycle, it is important to understand controls both of contemporary respiration fluxes and of how respiration and carbon cycling in soils would respond to a changing environment. The direct relationship between R_s and temperature is well documented (Flanagan and Veum, 1974; Swift et al., 1979; Nadelhoffer et al., 1991; Raich and Schesinger, 1992; Lloyd and Taylor, 1994; Peterjohn et al., 1994; Wüthrich et al., 1994; Simmons et al., 1996; Nakane et al., 1997; Bowden et al., 1998; Sylvia et al., 1998; Londo et al., 1999; Fang and Moncrieff, 2001; Rustad et al., 2001) and it is likely that warmer soils would result in more active soil organisms and increased decomposition rates. The longevity of such responses, however, and the broader implications for whole-ecosystem processes (and thus net

* Corresponding author. Tel.: +46-18-471-25-15; fax: +46-18-55-59-20.
E-mail address: sofie.sjogersten@geo.uu.se (S. Sjögersten).

0038-0717/02/$ - see front matter
PII: S0038-0717(02)00147-5

ecosystem CO_2 fluxes), will depend upon an array of additional factors; such as (i) the nature and properties (e.g. lability) of the soil organic matter (SOM) reservoirs, and how these modulate temperature responses and their variability through time (Liski et al., 1999; Ågren, 2000); (ii) the degree to which SOM is 'protected' from decomposition processes by complexation reactions with soil mineral material (Torn et al., 1997; Giardina and Ryan, 2000); (iii) whether temperature response kinetics are indeed even quasi-stable through time (Reichstein et al., 2000; Dalias et al., 2001), and (iv) whether interactions between soil moisture content and temperature can modify temperature response kinetics. Superimposed upon these broadly endogenous soil factors are those relating to how the autotrophs respond to changes in soil nutrient mineralisation and how these feed-forward to altered quality and quantity of plant litter and root activity (Chapin and Reuss, 2001).

High latitude soils (in boreal forest and tundra regions in particular) have occupied a central position in the debate on the potential impacts of environmental change on the global C cycle (Robinson and Wookey, 1997; Goulden et al., 1998; Christensen et al., 1999; Hobbie et al., 2000; Oechel et al., 2000). This interest has arisen due (i) to the very large accumulations of SOM in cold region soils (390 Gt C in tundra and boreal forest), (ii) the predicted greater-than-average climate warming at high latitudes, (iii) an hypothesised reduction in the degree to which SOM is 'stabilised' compared with warmer systems, and (iv) the hypothesised enhanced microbial responses to small changes in temperature and moisture in these systems.

Our aim in the current study was therefore to investigate the role of climate and initial soil characteristics in controlling soil CO_2 effluxes at the mountain birch forest–tundra ecotone in sub-arctic Sweden. The forest–tundra ecotone is of particular interest since models of the potential impacts of climate change on high latitude ecosystems predict that substantial areas of tundra will be replaced by boreal woodlands and forest (Emanuel et al., 1985; Kittel et al., 2000; White et al., 2000). Also, palaeoecological evidence (pollen and macrofossils) from Northern Sweden (Barnekow and Sandgren, 2001) indicates that during the early and mid Holocene (ca. 9350–5100 calibrated ^{14}C years before present) the mountain birch treeline extended 300–400 m above its present position in association with 1.5–2 °C warmer summer temperatures compared with today.

Climatic change will influence decomposition of SOM directly through the responses of the decomposer organisms to altered temperature and/or moisture regimes, but also indirectly through alterations in the structure and function of the broader ecosystem. Regarding the latter, we hypothesise that such alterations will be expressed most strongly where an ecotone shifts in location in response to environmental change. This may be particularly marked where the physiognomy of the vegetation is markedly different at one side of the ecotone compared with the other (e.g. forest–tundra). A shift from tundra to forest, or vice versa, will influence quality and quantity of litter inputs and thus soil chemistry (see Körner (1998) for a review), microclimate (e.g. through differential shading effects of the contrasting canopies, and/or alterations in snow-pack characteristics) and soil water regime (through differential interception by the canopy and contrasting evapotranspirative demand). Since R_s varies with vegetation (e.g. major biome types), and is positively correlated with mean annual temperature and mean annual precipitation (Raich and Schlesinger, 1992; Raich and Potter, 1995), we therefore hypothesise that respiration rates will vary substantially between contrasting ecosystems at the forest–tundra ecotone.

In northern Swedish Lapland tundra heath soils differ from the soils of adjacent mountain birch forest over very short distances (< 10 m; Per Thermaenius, unpublished data, see also Appendix A), both in terms of the thickness and structure of the organic horizon. The contrasting soil characteristics, vegetation cover and site microclimates of the forest and tundra heaths in close proximity to one another offer opportunities to answer some specific key questions: (1) What is the relative role of climatic factors versus SOM quality/quantity in controlling rates of R_s in the field? (2) Are temperature response kinetics of R_s temporally variable at the same site and are they dependent on the temperature range of the measurements? (3) To what extent can temperature response functions obtained in the field be reproduced under controlled conditions in laboratory-based incubations at a range of constant temperatures? We approached these questions by adopting in situ measurements of R_s in the field at both a forest and a tundra heath site, a reciprocal core transplant experiment across the forest–tundra ecotone (to separate climatic from SOM quality/quantity effects), and a laboratory incubation experiment at four contrasting temperatures incorporating Arrhenius-type temperature response evaluations at the close of the experiment. We confined our studies to soils from which living vegetation had been removed (thus R_s here comprised only heterotrophic respiration) as a practical consequence of not wishing to measure 'ecosystem respiration' (total autotroph and heterotroph respiration in the system). The implications of this are considered in Section 4.

2. Materials and methods

2.1. Study area

The study area is located in the sub-arctic/alpine treeline zone (mountain birch–tundra ecotone) in the Abisko area in northern Swedish Lapland at 68°21′N, 18°49′E. The area covers an undulating (although predominantly gentle: 4.8°) slope of northwesterly aspect, running ultimately to

the shore of Lake Torneträsk (341 m a.s.l.). The ecotone area in this region is composed of a patchwork of tundra and isolated extensions of mountain birch (*Betula pubescens* Ehrh. ssp. *czerepanovii* (Orlova) Hämet-Ahti) forest up to 700–800 m a.s.l.. The tundra areas are variable in species composition in relation to substrate characteristics, drainage and topography, although in this region there are substantial areas of mesic dwarf-shrub heath dominated by *Empetrum hermaphroditum*, *Vaccinium uliginosum*, *V. vitis-idea* and *Betula nana*, lichens (in particular *Cladonia* spp., *Nephroma arctica* and *Peltigera aphthosa*) and bryophytes (e.g. *Hylocomium splendens*, *Polytrichum* spp. and *Barbilophozia lycopodioides*). Mesic areas within the mountain birch forest have comparable understorey vegetation, although tending toward greater cover of *V. myrtillus*. The contemporary vegetation communities appear to have been rather stable since the mid Holocene (3500–4500 BP) (Barnekow, 1999; PhD Thesis) although a 20–50 m altitudinal advance of the alpine treeline in Abisko has been noted in association with a ca. 1.5 °C increase in mean annual temperature between 1900 and 1930 (Holmgren and Tjus, 1996), probably representing recovery following the Little Ice Age.

The bedrock is mainly hard-shale but outcroppings of some richer bedrock types, such as marble and amphibolites, are present in the area. The small-scale topography is dominated by hummocky till deposits. At Abisko Scientific Research Station (365 m a.s.l.) the mean January and July temperatures are −11.9 and 11.0 °C, respectively, and the annual precipitation 304 mm (1961–1990 mean; Alexandersson et al., 1991). The sites are well drained to mesic and the soils, although thin, are spodosols (principally orthods) developed within medium to coarse-grained till deposits. Soil pH in the O/A horizons is moderately acid (pH 4–4.5). At both sites soils have similar moisture-content, texture and underlying bedrock, although the structure and chemistry of the organic horizon differs between the two sites (Appendix A) (Sjögersten et al., 2002; Per Thermaenius, unpublished data). In the forest the soil organic horizon is thinner (ca. 5 cm deep), more fibrous, of lower density and has a lighter, more reddish, colour (Munsell colour: 5YR 2/3–2/4 very dark reddish brown). No clearly developed humic horizons were found at the forest site. At the tundra site, the average soil organic horizon is ca. 8 cm deep with separate F- and H-horizons, and the colour is very dark brown (Munsell colour: 7.5YR 2/3). Soil descriptions are given in Appendix A. Additional measurements of the depth of the organic horizon were made on the soil cores used in the laboratory experiment described later.

2.2. Experimental design

2.2.1. Soil transplant experiment

In July 1999 we established two experimental sites around the mountain birch–tundra ecotone. The forest site was situated well within the continuous woodland at 500 m a.s.l., and the open tundra heath was situated within generally continuous tundra at 620 m a.s.l.. At each of the sites we selected 20 experimental plots, and from each of these plots a soil core was taken using a purpose-built stainless steel corer housing polycarbonate sleeves 10 cm deep and 15 cm in diameter. During coring soil monoliths were fitted exactly into the polycarbonate sleeves. Of these 20 soil cores at each site 10 were placed back into the soil, as controls (still in the sleeves), but in a different position. The remaining 10 cores were transported from the original site to the forest or tundra site, respectively, where they were inserted (also in the sleeves) into the holes remaining from the cores taken at that site. Before inserting the soil cores we clipped the above ground vegetation; this was to allow R_s to be measured subsequently, rather than ecosystem respiration (any re-growth was also clipped during the course of the experiment). When placing the soil cores back into the ground we ensured good contract between the base of the soil core and the surrounding soil to minimise the effect on soil drainage and heat transport.

Soil respiration rates were measured in the field on six occasions in July 1999, soon after the experiment was established, to record the initial response to the actual coring and re-location procedure. In September, at the end of the frost-free season, measurements were made when soil temperatures had dropped to ca. 5 °C. During 2000 soil respiration was measured on a weekly basis on 12 occasions from 16 June (just after snow melt at the forest site) to 7 September (when the soil temperatures had dropped substantially). The 2001 measuring period was focused on three occasions in July. For the soil respiration measurements we used a portable Infra Red Gas Analyser (IRGA; EGM 2), with a cylindrical cuvette (CPY-2) placed on the soil core (PP Systems, Hitchin, Hertfordshire, UK). The IRGA was calibrated using a 498 ppmv carbon dioxide standard. We also measured soil water content (integrated over 0–10 cm depth) with a ThetaProbe and hand-held ThetaMeter (Delta-T Devices, Burwell, UK), with three replicates around each plot, and soil temperature at 5 cm depth, while the R_s measurements were made.

2.2.2. Soil incubation experiment

In July and August 1999 we 'pre-sampled' 48 soil cores (24 each from the forest and tundra) for an incubation experiment under controlled temperature conditions in the laboratory. This procedure involved taking cores but then replacing them immediately in the ground in situ until the end of the season. The pre-sampling allowed rapid collection of the cores in September, followed by transport (refrigerated) to the laboratory in Uppsala where the cores were stored at 2 °C for ca. 2 months (due to practical constraints) before the experiment commenced. Both as a reasonable approximation of autumn temperatures in these systems, and also to reduce metabolic rates (and thus minimise depletion of labile C pools) without the use of

freezing 2 °C was chosen. Prior to the experiment we clipped the vegetation from the cores and fixed an inert polyethylene mesh (2 mm) to the base of each core to prevent loss of soil upon handling. The cores were subsequently watered to field capacity, and they remained in the polycarbonate sleeves throughout the experiment. During the first week of incubation the temperature for all cores was maintained at 7 °C (the thaw season average temperature at the sites of origin) and the soils were left to equilibrate. After a week of incubation at 7 °C two initial respiration measurements were made. After the initial measurements we blocked the soil cores randomly into six different groups according to their initial respiration rate. Six replicates of each soil, one from each blocking group, were then placed in incubators with constant temperatures at 2, 7, 12 and 17 °C. We chose these temperatures to simulate both cooling and two levels of warming compared to the ambient growing season average.

We measured soil respiration rates over a 10 week period; the measurements were repeated on 13 occasions, with a higher frequency at the start of the experiment. At the end of the experiment we measured the temperature response of the soils from each incubator (i.e. 2, 7, 12, 17 °C) over five temperatures, 2, 7, 9.5, 12, 17 °C, each temperature step lasting 24 h. Responses were measured with both ascending and descending temperature steps, although only data from ascending temperatures are presented subsequently.

We used the same infra red gas analyser as described above to measure soil respiration rates in the lab. The measuring period was 120 s and each measurement was repeated twice. The soil cores were kept moist and were always watered with deionised water to field capacity 1 day prior to measurements.

2.3. Analyses

2.3.1. Total microbial biomass C

At the end of the incubation experiment we measured total microbial biomass in the samples by fumigation–extraction (Vance et al., 1987) and analysed the extracts for total organic carbon (TOC). Fresh soil samples, taken through the entire depth of the soil core, were sieved to pass 4 mm (this mesh size was chosen to reduce physical disturbance of fungal hyphae) and then 15 g sub-samples were fumigated in a chloroform atmosphere for 24 h. Control and fumigated samples were extracted in 50 ml 0.5 M K_2SO_4 by shaking for 30 min and then filtered through Whatman 42 filterpaper. The extracts were stored at 5 °C and were analysed for TOC the following day on a Shimadzu TOC-5000 with a Shimadzu ASI-5000 auto-sampler/autoinjector. The samples were burnt catalytically at 680 °C in 150 ml min^{-1} flow of purified air. Carbon dioxide was detected specifically by NDIR (Non-Dispersive Infrared)-detector.

2.3.2. C, N content

Total carbon and nitrogen content of bulk SOM were determined simultaneously using a Carlo-Erba model NA2000 nitrogen analyser.

2.3.3. Statistical analyses

We used repeated measures analysis of variance (ANOVA) to test for effects of the treatments (transplantation/warming), site (and thus contrasting vegetation types) and time. Where significant differences between sites and time were indicated by ANOVA, we used a post hoc means separation test (Tukey's HSD (Honest Significant Difference)) to determine which comparisons were significant.

For the entire seasonal data set we used multiple regression analysis to test the effects of soil volumetric water content and temperature on CO_2 fluxes. General linear models (GLM) were used to test for the effects of temperature. Statistical analyses were performed using STATISTICA (StatSoft, 1995).

We used both Arrhenius plots and Q_{10} (temperature coefficient; where $Q_{10} = (R_{T+10}/R_T)$ analysis to evaluate the effect of temperature on the R_s rates measured both in the incubation experiment and also in the field. For the field experiment monthly Q_{10} values were calculated. According to model and Q_{10} analysis by Fang and Moncrieff (2001), the Arrhenius model is better than other suggested relationships between R_s rates and temperature due its performance and theoretical basis in thermodynamics. Lloyd and Taylor (1994) also concluded that linear and exponential (Q_{10}) functions are inferior to Arrhenius-type equations wherein the activation energy for respiration varies inversely with temperature. In other words, the relationship between respiration and temperature is not a simple exponential across the normal range of physiological temperatures. The main problem with Arrhenius-type equations for our analyses, however, is the slight underestimation of respiration rates at low temperatures. Recognising the advantages and limitations of each form, we have chosen to apply both, where appropriate, for comparative purposes.

The Arrhenius curves are constructed by plotting the natural logarithm of the soil respiration rates (k) against the inverse of temperature, and the equation can be written

$$\ln k = \ln A - E_a/RT$$

or

$$k = A\, e^{-E_a/RT}$$

where E_a is the activation energy and A is called the pre-exponential, or frequency factor (interpreted as the frequency of collision of reacting molecules; Panikov (1997)). The slope of the Arrhenius plot gives $-E_a/R$ (kJ mol^{-1}) and the intercept at $1/T = 0$ gives $\ln A$.

3. Results

3.1. Soil transplant experiment

The soil respiration rates at control plots (native soils in situ) were significantly ($P < 0.005$) higher at the forest site compared to the tundra site during the 1999–2001 measuring period (Fig. 1 shows data for 2000). Average fluxes over the 2000 thaw season were 0.62 and 0.48 g CO_2 m^{-2} h^{-1}, at forest and tundra control plots, respectively. The transplanted soils responded in a significant way to transplantation to a new environment (Fig. 1). The tundra soils transplanted to the forest site increased their respiration rate to 0.68 g CO_2 m^{-2} h^{-1} ($P < 0.05$), i.e. a 42% increase compared to the tundra control plots, and no significant difference was found between the forest control plots and the transplanted tundra soils. Conversely, the transplanted forest soils had significantly reduced respiration rates: 0.45 g CO_2 m^{-2} h^{-1} ($P < 0.05$), i.e. 28% less compared to control plots. Again, at this site, no significant difference was found between the tundra control plots and the transplanted forest soils. Average soil temperature (5 cm) and soil water content (integrated 0–10 cm) for the 2000 measurement period was 8.2 °C and 0.24 m^3 H_2O m^{-3} soil; and 7.5 °C and 0.31 m^3 H_2O m^{-3} soil; for the forest and tundra site, respectively.

Soil respiration rates varied significantly ($P < 0.005$) over time in both 1999 and 2000. In 2000, the year with weekly measurements over the whole season, the highest R_s values were recorded in the latter half of July and beginning of August, and the lowest at the beginning and the end of the measurement periods (Fig. 1). The initial CO_2 pulse in July 1999 is attributed to increased microbial activity in the soil due to root decay, as well as the decomposition of damaged mycorrhizial mycelium, following clipping of the above-ground vegetation. We have therefore based our seasonal fluxes on measurements from the 2000 thaw season when the effect of the initial disturbance had decreased.

According to multiple regression analysis with soil water content and soil temperature as independent variables, 28 and 45% of the variance ($P < 0.001$) in soil respiration rates at control plots is explained at the forest and tundra site, respectively. Temperature explains a larger proportion of the variance than soil water content in both cases ($BETA_{soil\ temperature\ (forest)} = 0.47$; $BETA_{soil\ water\ content\ (forest)} = 0.28$; $BETA_{soil\ temperature\ (tundra)} = 0.69$; $BETA_{soil\ water\ content\ (tundra)} = 0.27$). In the range of measured soil temperatures and soil water contents, higher values of these parameters generally increase soil respiration rates. Soil water contents were, however, negatively correlated with soil temperature at the tundra site ($R^2 = 0.07$, $P < 0.01$) and at the forest site a significant regression between soil moisture and soil respiration was noted, albeit with a low regression coefficient ($R^2 = 0.06$, $P < 0.05$). A marked reduction in soil water content in the end of July 2000 thus significantly

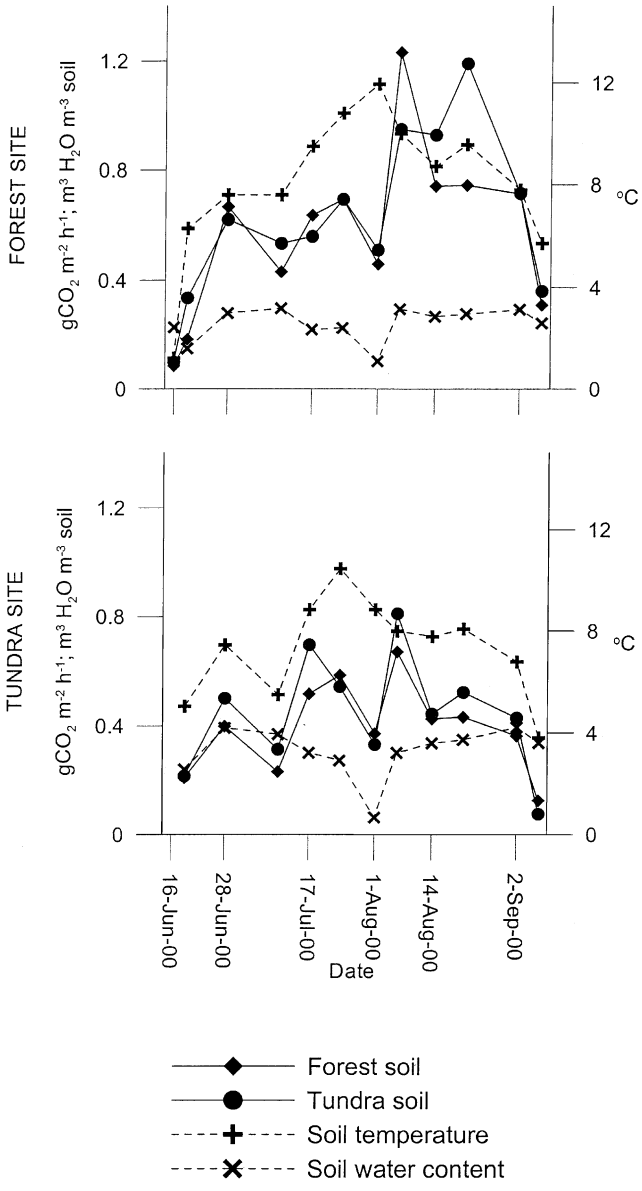

Fig. 1. Soil respiration rates (mean values, $n = 10$) measured in the field during the 2000 thaw season from forest and tundra sites at both control plots and plots with transplanted soils. The figure also presents soil temperatures at 5 cm depth (scale on the right hand axis) and soil moisture integrated over the top 10 cm (scale on the left hand axis).

($P < 0.005$) reduced soil respiration rates, especially at the forest site.

Best-fit equations for the temperature and respiration regressions were a secondary polynomial ($R^2 = 0.39$) at the tundra, and a linear regression ($R^2 = 0.21$) at the forest (Fig. 2 (a) and (b)). The polynomial for the tundra site describes a nearly linear relationship between 3.5 and 7.0 °C, while above 7 °C the soil respiration rate was less responsive to increased soil temperature. The Arrhenius equations for soil respiration are given in Fig. 2 (c) and (d)) and Table 1. The Arrhenius equation explains 37% of the variation in the tundra soil respiration and 42% for the forest soils. The activation energy (derived from the slope in

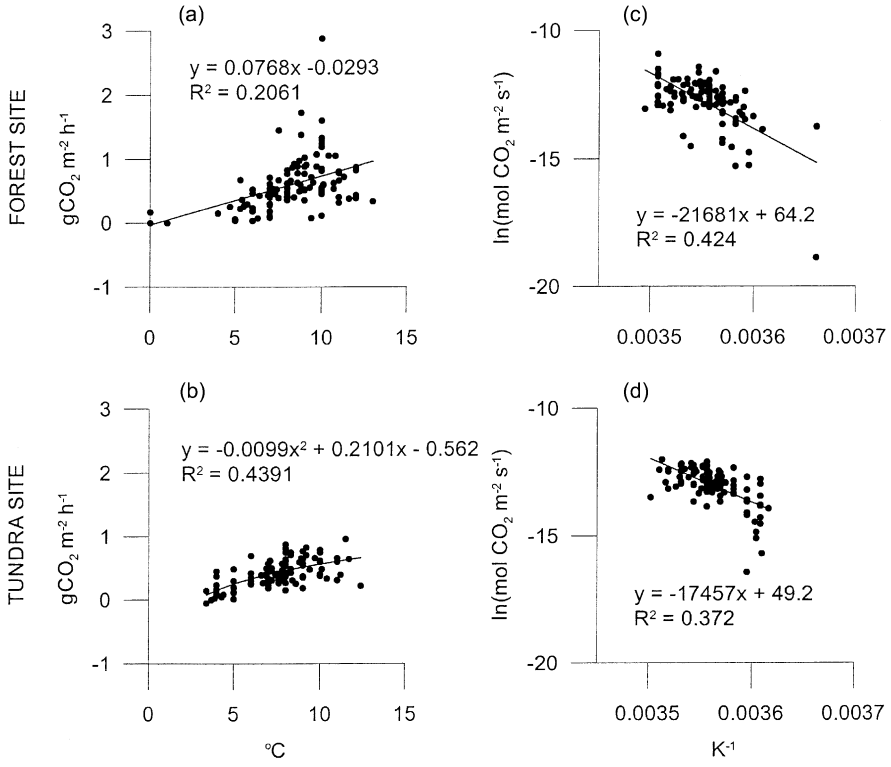

Fig. 2. (a) and (b) Best-fit regression between soil respiration rates and soil temperature from forest and tundra control plots during the 2000 measuring period in the field. (c) and (d) Arrhenius plots with fitted Arrhenius equations from forest and tundra control plots during the 2000 measuring period in the field.

the Arrhenius plots) was higher in forest soils c ompared to tundra soils; 180.2 and 145.1 kJ mol^{-1}, respectively. The R^2 values were generally lower for transplanted soils; 30 and 19, for tundra and forest soils, respectively. For the transplanted soils activation energy was lower compared to control soil, 122.9 and 73.1 kJ mol^{-1}, in forest and tundra soils, respectively.

Q_{10} values calculated over different months were generally higher when temperatures were low, i.e. in June and September, although it should be noted that there was only one interpretable result for September (Table 2). No significant difference between forest and tundra soil, or control and transplanted soils, could be detected. The lower Q_{10} values in mid summer reflect the reduced significance of temperature (low R^2 values, see Fig. 3) in July and August, when low soil moisture content instead seems to constrain soil respiration rates. Table 2 also shows that the relationship between soil respiration rates and temperature was rather similar for soils incubated at their original site and at a new location when Q_{10} values were low in July and August.

3.2. Laboratory incubation experiment

Forest soil respired significantly ($P < 0.01$) more than tundra soil over the 10 week incubation period (0.26 and 0.20 g CO_2 m^{-2} h^{-1}, respectively) when averaged over all different temperature regimes (2–17 °C) (Fig. 4). Soils

Table 1
Arrhenius equations derived from the field experiment in Swedish Lapland (data from the whole 2000 measuring period), activation energies calculated from the transplant experiment. The equations are derived from GLM analysis of the data set, p_i (p-value intercept); p_s (p-value slope)

	Arrhenius equation		Activation energy (kJ mol^{-1})	
	Forest soil	Tundra soil	Forest soil	Tundra soil
Forest site	$y = -21681x + 64.2$ $R^2 = 0.4240$, $F = 80.3$ $p_s < 0.001$, $p_i < 0.001$	$y = -8796x + 18.6$ $R^2 = 0.1933$, $F = 25.7$ $p_s < 0.001$, $p_i < 0.001$	180	73
Tundra site	$y = -14790x + 39.6$ $R^2 = 0.3040$, $F = 70.2$ $p_s < 0.001$, $p_i < 0.001$	$y = -17456.8x + 49.2$ $R^2 = 0.3720$, $F = 57.5$ $p_s < 0.001$, $p_i < 0.001$	123	145

Table 2
Monthly Q_{10} values from the 2000 field season, calculated from regression models (ΔT 10 °C around the season mean temperature, i.e. 7.85 °C) at the forest and tundra site, both controls and transplanted soils

Month	Forest soil (Q_{10})		Tundra soil (Q_{10})	
	Control	Transplanted	Control	Transplanted
June	39.4	6.3	10.9	6.9
July	7.6	7.4	2.8	2.7
August	0.7	0.9	1.2	0.4
September	∞[a]	6.0	∞[a]	∞[a]

[a] ∞ values result from our regression models approaching zero R_s at low soil temperature and should not be over interpreted.

incubated at the two lower temperature regimes (2 and 7 °C) respired at significantly lower rates than the two higher (Figs. 4 and 5). The two lower temperatures, however, were neither significantly different between the two regimes, nor between the different soil types. The respiration rate from the tundra soil incubated at 12 °C differed significantly ($P < 0.05$) from all other combinations of soil type and temperature treatment. We obtained generally higher respiration rates from the field measurements compared to the incubation experiment despite a higher 'mean experiment temperature' from the incubation experiment. This is probably due to the removal of respiration at depth in the incubation experiment, where the soil cores were only 10 cm deep at maximum (Per Thermaenius, unpublished data 2001).

When average respiration rates from the 10 week incubation are plotted against incubation temperature the two soil types have a near-significant ($P = 0.073$) difference in temperature response, with a more S-shaped response for the forest soil compared to a more linear temperature response for the tundra soils (Fig. 5(a)), suggesting a threshold value between 7 and 12 °C for the forest soil. The Q_{10} values calculated from the incubation experiment are presented in Table 3. These values were calculated over a 5 °C range (i.e. 2–7, 7–12, 12–17 °C). For the whole 10 week experiment, Q_{10} values obtained from the 7–12 °C range were significantly ($P < 0.001$) higher than the 2–7 and 12–17 °C temperature ranges, and no significant differences between soil types were detected.

Arrhenius equations gave good fits between temperature and soil respiration from the incubated soils when the temperature response kinetics were investigated at the end of the experiment (Table 4). No significant difference between rising and falling temperature responses was noted after 10 weeks of incubation. The activation energies calculated from the Arrhenius equations are generally lower for the soils incubated at 2 and 7 °C. The pattern is clearest for forest soils, but the tendency is still there for tundra soils.

After the initial increase in soil respiration following exposure of the soil to the different incubation temperatures no significant variations in soil respiration rates were measured over time. No signs of labile carbon depletion were detected (i.e. there were no reductions in respiration rates through time), neither from the measurements repeated over 10 w of incubation, nor from the Arrhenius curves constructed at the end of the experiment.

The total microbial biomass C was significantly ($P < 0.01$) larger in the tundra soils compared with the forest soils (3.4 and 2.0 mg microbial C g^{-1} dry soil, respectively). There was no significant relationship between the soil respiration rates and the total microbial biomass in each sample at the end of the experiment (Fig. 5), neither between microbial biomass and temperature and depth of the organic horizon, respectively.

4. Discussion

Both the transplant experiment and the laboratory incubation experiment show that mountain birch forest has higher R_s rates compared to tundra heath (ca. 30 and 20% higher in the field and incubation studies, respectively). The fluxes measured in the forest and tundra control plots (0.62 and 0.48 g CO_2 m^{-2} h^{-1}, respectively) during the 2000 growing season compare with values of 0.8 g CO_2 m^{-2} h^{-1} measured in mountain birch forest at lower altitude (450 m a.s.l.) in the Abisko Nature Reserve (Rustad et al., 2001). The latter flux rates are rather high compared with a wide range of sub-arctic and arctic sites (Rustad et al., 2001) and are more similar to respiration data from boreal forest and woodlands according to Batjes and Bridges (1992) and Raich and Schlesinger (1992). This suggests favourable conditions for decomposition in these mesic sub-arctic soils, and relatively rapid (i.e. decadal scale) carbon and nutrient turnover in the area. The results from the soil transplant experiment (Figs. 1–3; Tables 1 and 2) suggest that the physical environment (i.e. soil temperature and soil water content) at recipient sites overrides controls exerted by initial SOM quality and microbial community/biomass on R_s. Both the transplanted soil types adjusted to respiration rates comparable to those measured at the control (recipient) plots at each site (Fig. 3). The increase in R_s noted for the tundra soils to rates comparable with those of the forest control plots when positioned in a forest environment, and the maintenance of this increase throughout the 2000 measuring period (and into the summer of 2001), as well as the higher SOM and C content of the tundra soils compared with the forest (Appendix A), confirm that there is a pool of labile C in the tundra soil that could be accessed rapidly in a more favourable environment.

A clear methodological constraint with our measurements of R_s, both in the field and in the laboratory, is that we cannot evaluate the significance of root respiration and rhizosphere processes, including mycorrhizae. Although we noted minor re-growth in some of the cores, mainly of

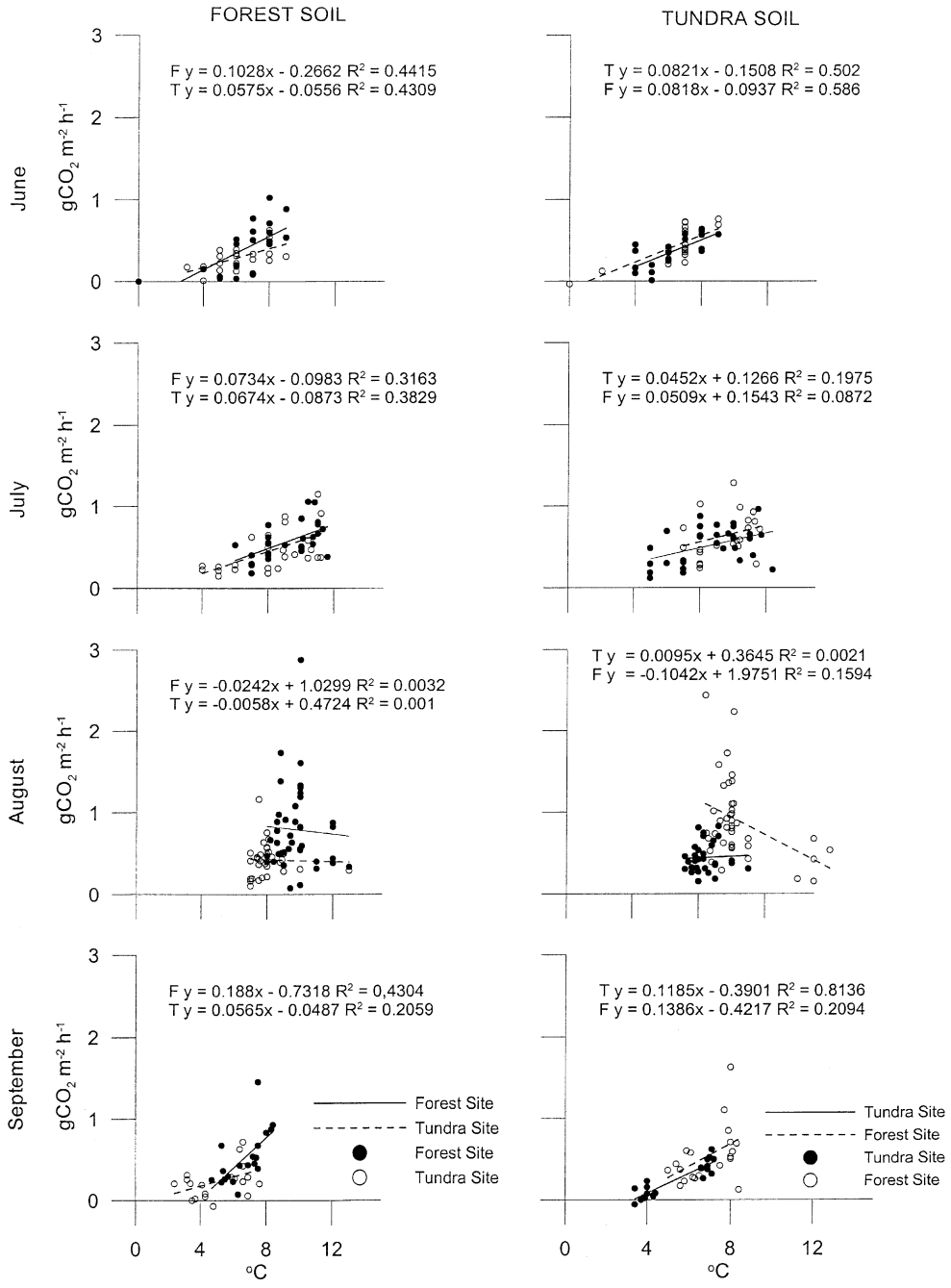

Fig. 3. Respiration rates of forest and tundra soils at both sites (i.e. both control and transplanted soils) in the field plotted against temperature for each of four months separately during the 2000 thaw season. For each month and soil type (forest or tundra) a regression model was constructed, which was used for calculation the monthly Q_{10} values presented in Table 2.

V. myrtillus, indicating that some below-ground plant parts were still alive, we assume that most of the fine roots as well as mycorrhizae had died before or during the 2000 and 2001 field measurements. Thus we assume that our measurements mainly reflect the responses of decomposer heterotrophs to environment, and were not strongly influenced by autotrophs. Whilst this simplifies our interpretation to some extent, we cannot ignore the significance of rhizosphere processes, and both ecto- and ericoid mycorrhizae, for overall decomposition processes and nutrient recycling in these and similar ecosystems (Bååth and Söderström, 1979; Smith and Read, 1997). We also note the strong dependence of soil respiration on rates of photosynthesis observed in a study of Swedish boreal forest (Chapin & Ruess, 2001; Högberg et al., 2001). Clearly, therefore, our results must be interpreted cautiously since they do not reflect overall soil respiration. In late July 2001, however, we compared R_s measured in the field (using the clipped

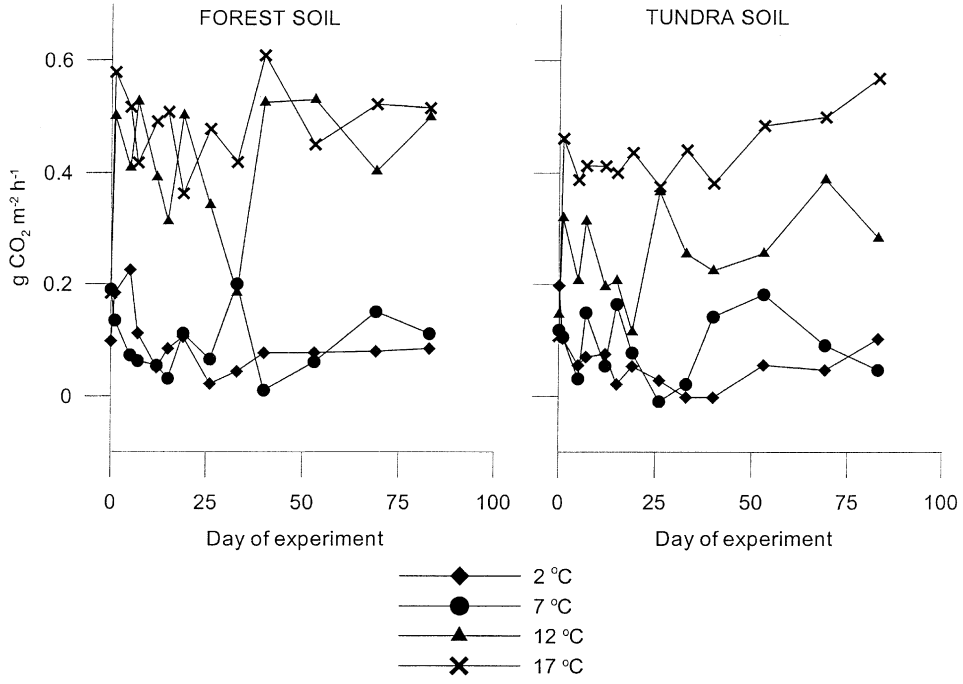

Fig. 4. Soil respiration rates measured over the 10 week laboratory-based incubation of forest and tundra soils, in four different temperature regimes (2, 7, 12 and 17 °C); 7 °C is close to the growing season average temperature.

cores) with ecosystem respiration rates (measured in the dark) of adjacent unclipped areas with intact vegetation; ecosystem respiration (total heterotroph and autotroph) was 15–18% higher than our measured R_s (S. Sjögersten, unpublished data), but this modest increment suggests that the contribution of autotrophs and mycorrhizae to soil respiration at our plots was substantially lower than that observed by Högberg et al. (2001) in boreal forest 4° of latitude further south. This is, nonetheless, a key issue, and more attention must be focused upon evaluating differential environmental controls upon the respiration of root systems, mycorrhizae and other heterotrophic decomposer organisms, and the relative magnitudes of these processes in contrasting ecosystems.

The strong relationship between soil temperature, soil moisture and R_s rates has been demonstrated in many field experiments in a wide range of ecosystems (Peterjohn et al., 1994; Wüthrich et al., 1994; Simmons et al., 1996; Nakane et al., 1997; Bowden et al., 1998; Londo et al., 1999). Generally soil temperatures are the principal controlling factor in mesic soils, while extremes (wet or dry) of soil water content tend to reduce R_s rates (Flanagan and Veum, 1974; Peterjohn et al., 1994; Simmons et al., 1996; Dong et al., 1998; Bowden et al., 1998). These statements agree well with the results from the mesic freely drained soils in our study, where temperature is the main controlling factor but soil moisture affected R_s rates (negatively) mainly after a prolonged dry period.

In the literature it is frequently stated that soils in cold environments are more sensitive to changes in temperature compared to soils in more favourable environments (Swift et al., 1979; Anderson, 1991; Lloyd and Taylor, 1994). This view has, however, been challenged recently by a meta-analysis of soil warming experiments conducted by Rustad et al. (2001). The analysis revealed that forest ecosystems generally exhibited a greater response to experimental warming compared with tundra and grassland systems. In our study, the monthly Q_{10} values calculated from the field experiment were variable but there is a clear tendency toward higher Q_{10} values at low temperatures, with the highest Q_{10} values at the beginning and end of the measuring period (Table 2). During July and August the importance of temperature decreased markedly and other parameters, such as soil water content, assumed increased significance in controlling the flux rates (Fig. 3). Similar temperature-dependency of Q_{10} values has been observed by Schleser (1982), Lloyd and Taylor (1994) and Widén (2001), the latter also finding higher Q_{10} values in the beginning of the growing season in a boreal forest when temperatures were low. Our data strongly support the view that Q_{10} values are not an inherent and fixed property of a soil; they vary over a season as the importance of temperature to R_s varies. Compared to the 2.4 global median Q_{10} value (Raich and Schlesinger, 1992) our values are generally high (with the exception of the August 2000 field data), suggesting a greater influence of temperature on R_s in these cold ecosystems than the global average (Table 2).

The higher R_s for forest compared to tundra soils at all temperatures in the incubation experiment (Fig. 4) implies

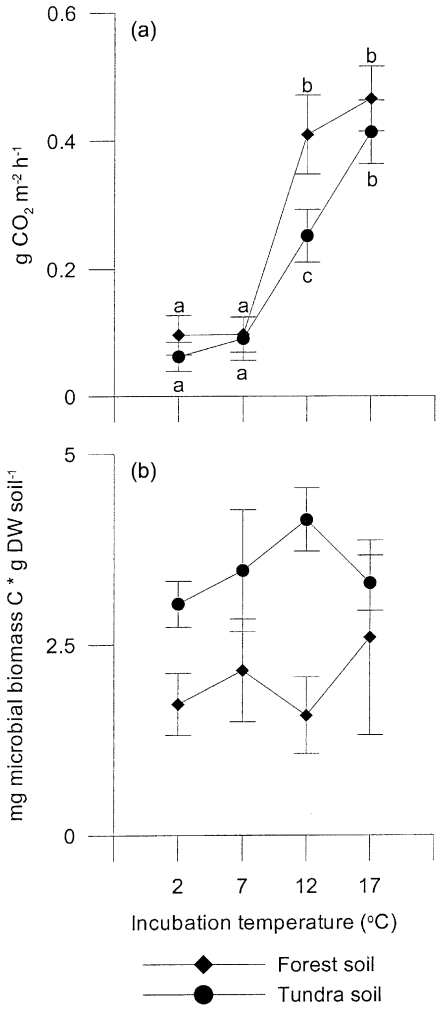

Fig. 5. (a) Relation between average soil respiration rates, measured over 10-weeks in the laboratory, and incubator temperature for forest and tundra soils. Symbols accompanied by different letters are significantly different at $P < 0.05$ based upon ANOVA and means separation test; (b) microbial biomass measured at the end of the experiment in forest and tundra soils. Mean values (± SEM) are shown.

that there exists a substrate quality difference, with more labile carbon or a more efficient/active decomposer community, in the forest soil compared with the tundra. This agrees with the observation by Raich and Tufekcioglu (2000) that litter production and soil respiration are positively correlated in mature forest systems. The same situation is likely in our study ecosystems, where we hypothesise that the birch forest produces significantly more litter with more labile chemistry compared to tundra. We note, however, that tundra soils transplanted into forest adopted consistently higher respiration rates than at the site of origin (Fig. 1), indicating that a labile pool of carbon is available in these soils too. Thus a simple interpretation of SOM lability in the contrasting soils is not justified.

The Arrhenius curves resulting from the field and incubation experiment (Tables 1 and 4, respectively) point toward lower activation energies for soils incubated at lower temperatures, suggesting that these soils need less kinetic energy (i.e. temperature) to drive metabolic processes. This is consistent with the view that microorganisms with more efficient enzymatic systems are active at lower temperatures, and may point to a shift in microbial community towards more psychrophilic organisms, or a physiological acclimation of the existing community (Panikov, 1997). Our results on activation energies contrast, however, with the analysis by Lloyd and Taylor (1994) who found generally higher activation energies for soils in cold environments compared to warmer (in an evaluation of 15 soil respiration studies conducted in a variety of ecosystems and biomes). The data for microbial biomass at the end of the incubation (Fig. 5) suggests that the increased R_s rate as a response to temperature is caused by increased metabolic efficiency rather than a larger microbial population. The larger microbial biomass in the tundra soils (with a lower respiration rate cf. forest) at the close of the experiment compared to forest soils suggests that, in this case, microbial efficiency and resource quality is more important to the total R_s than the actual population size (Fig. 5). Vance and Chapin (2001), in an analysis of soil microbial activity in contrasting Alaskan taiga forest systems, also noted that microbial biomass is not strongly coupled to indices of microbial activity (such as R_s).

The temperature response curves in our experiments do not follow the exponential relationship reported in many investigations (e.g. Peterjohn et al., 1994; Simmons et al., 1996; Bowden et al., 1998; Davidson et al., 1998; Londo

Table 3
Q_{10} values calculated from temperature response measured at the end of the incubation period in the laboratory for soils incubated at four temperatures

Incubation temperature (°C)	Tundra soil (Q_{10})			Forest soil (Q_{10})		
	7–2	12–7	17–12	7–2	12–7	17–12
10-weeks average	1.3 ± 0.2	7.4 ± 1.0	1.6 ± 0.3	2.8 ± 0.5	6.7 ± 1.8	2.4 ± 0.3
2	3.3 ± 1.1	5.6 ± 0.8	2.4 ± 0.2	5.3 ± 2.2	2.8 ± 0.6	6.9 ± 4.2
7	4.8 ± 2.1	4.5 ± 2.5	2.9 ± 0.7	3.7 ± 2.2	3.6 ± 0.8	2.6 ± 0.3
12	3.9 ± 1.3	6.0 ± 1.7	2.3 ± 0.3	14.0 ± 4.7	3.6 ± 0.9	3.6 ± 1.0
17	4.5 ± 1.9	15.3 ± 10.0	3.5 ± 0.8	5.7 ± 1.0	3.6 ± 0.8	3.8 ± 0.9

Occasional apparently negative and zero respiration values were excluded from the data set as they are considered the result of analytical constraints near the detection limit of the IRGA. Top row: Q_{10} values calculated from the incubation experiment. The values are averages (± SEM) for the whole incubation period (i.e. 10 weeks) and have been calculated by dividing the average respiration rate at 7 and 2, 12 and 7, and 17 and 12 °C.

Table 4
Arrhenius equations from the temperature kinetics investigation ending the 10-weeks incubation period, equations are given for each temperature treatment and soil type. The equations are derived from GLM analysis of the data set; $n = 6$; p_i (p-value intercept); p_s (p-value slope)

Incubation temperature	Arrhenius equation		Activation energy (kJ mol^{-1})	
	Forest soil	Tundra soil	Forest soil	Tundra soil
2 °C	$y = -11298x + 26.6$ $R^2 = 0.51$; $F = 29.5$ $p_s < 0.001$, $p_i < 0.001$	$y = -11587x + 27.2$ $R^2 = 0.67$; $F = 52.8$ $p_s < 0.001$, $p_i < 0.001$	94	96
7 °C	$y = -11038x + 25.3$ $R^2 = 0.62$; $F = 46.2$ $p_s < 0.001$, $p_i < 0.001$	$y = -11813x + 27.7$ $R^2 = 0.49$; $F = 25.3$ $p_s < 0.001$, $p_i < 0.01$	92	98
12 °C	$y = -15982x + 43.3$ $R^2 = 0.75$; $F = 82.1$ $p_s < 0.001$, $p_i < 0.001$	$y = -13144x + 33.1$ $R^2 = 0.82$; $F = 124.5$ $p_s < 0.001$, $p_i < 0.001$	133	109
17 °C	$y = -13797x + 35.2$ $R^2 = 0.85$; $F = 162.3$ $p_s < 0.001$, $p_i < 0.001$	$y = -13241x + 33.3$ $R^2 = 0.52$; $F = 30.4$ $p_s < 0.001$, $p_i < 0.001$	115	110

et al., 1999). At both sites a near-linear relationship between R_s and soil temperature over the measured temperature range was found, with indications of a slightly stronger control on R_s at lower soil temperatures at the tundra site in both the field and laboratory experiment (Figs. 2, 3 and 5). These relationships possibly indicate an adaptation of the decomposer community to the cold environment, particularly in the tundra soils, to maximise the benefit of a small temperature increase within the lower temperature range. The apparent sinusoidal temperature response of the forest soils in the incubation experiment (Fig. 5) is interesting because the threshold value seems to be just around the ambient summer temperatures. This gives potential for increased soil respiration rates in response to quite small increases in soil temperatures, and this interpretation is also consistent with the small difference in temperature between tundra and forest plots in the field during 2000 (7.5 and 8.2 °C, respectively). A similar threshold value was identified in a study of Arctic soil by Nadelhoffer et al. (1991) at around 9 °C (also the upper range of the daily temperatures). Above this threshold soil respiration increased by a factor of two compared to the ambient situation. This might indicate that soil microorganisms are particularly sensitive to temperatures outside the normal range, or that the microbial community at higher temperatures shifts in favour of organisms with a different temperature response. The impact of such a threshold must, however, be considered in the context of soil moisture conditions: In the incubation experiment soil moisture was held at field capacity across all temperatures. Our field experiment, however, showed a significant relationship between increased soil temperature decreased soil moisture content, and reduced R_s. This suggests that the impact of increased soil temperature on R_s rates could be significantly constrained by soil moisture content in these environments. Similar findings of moisture controls on R_s in dwarf-shrub heath soils have been presented by Illeris (2001, PhD Thesis).

We conclude that a shift from tundra to birch forest would result in an initial pulse of carbon released from soil to the atmosphere as labile SOM stored in tundra soils is used by the decomposer community. Data from both the field experiment and the controlled incubation show that these soils are highly sensitive to increasing temperature, but that the responses: (i) vary temporally through the thaw period, and (ii) are not independent of changes in soil moisture content even in this maritime climatic setting. Since changes in temperature and precipitation will likely co-vary in this and other high-latitude regions (Overpeck et al., 1997; Stötter et al., 1999) our data underscore the importance of improving models of soil hydrological status for understanding decomposition processes and R_s (Hodkinson et al., 1999). Contrasts in the detailed form of the relationships between temperature and soil respiration observed in the field experiment and the controlled incubation may, to some extent, reflect the fact that: (i) soil moisture status and temperature were kept constant in the laboratory, and (ii) mineralisation products of decomposition remained in situ within the incubation cores. Both factors could have affected the dynamics of decomposer metabolism and the community composition/turnover in the field compared with the laboratory. The data illustrate the potential risks of purely field or laboratory-based investigations, and we note the tendency (highlighted by Kampichler et al. (2001)) for soil ecological research to have become over dominated recently by short-term experiments involving micro and mesocosms in the laboratory.

Table A1
Soil profile descriptions. Two soil profiles (i) and (ii) were described at each site

	Horizon	Depth (cm)	Colour	Texture	%C	%N	%P	pH	Density (g cm^{-3})	LOI (%)
Tundra (i)	Organic	0–8	5 YR 3/3	Felty				4.53	0.15	78
	Albic	8–11	10 YR 5/4	Gravely sand				5.09	1.14	6.0
	Spodic	11–21	7.5 YR 5/6	Gravely sand				5.55	0.74	20
Tundra (ii)	Organic	0–7	7.5 YR 2/3	Felty				3.86	0.14	96
	Oi	0–1			46.13	1.17	0.90			
	Oe	1–5			40.52	1.33	1.06			
	Oa	5–7			38.48	1.27	0.90			
	A	7–9	7.5 YR 4/3	Silt				4.35	0.34	50
	Albic	9–13	10 YR 5/2	Silt				5.14	0.84	5.6
	Spodic	13–16	10 YR 4/6	Sandy gravel				5.61	1.73	1.0
	C		7.5 YR 3/3	Sandy gravel				6.22	1.66	0.71
Forest (i)	Organic	0–5	5 YR 2/4	Fibrous				5.22	0.066	94
	Oi	0–0.2								
	Oe	0.2–4.8								
	Oa	–								
	Albic	5–8	2.5 YR 5/2	Sandy silt				4.20	1.47	5.2
	C	8–33	2.5 YR 4/3	Silt				5.58	1.10	1.1
Forest (ii)	Organic	0–5	5 YR 2/3	Fibrous				4.07	0.11	96
	Oi	0–0.5								
	Oe	0.5–2.5			29.6	1.40	0.91			
	Oa	2.5–5			41.7	1.87	0.83			
	Albic	5–20	5 Y 6/2	Heterogen silt				4.95	1.30	2.2
	C	20–29	5 Y 4/3	Sandy silt				5.91	1.68	1.3

Acknowledgments

We thank the European Commission IVth Environment and Climate Framework Programme, the Swedish Natural Environment Research Council (Naturvetenskapliga Forskningsrådet—NFR; now Vetenskapsrådet), the Swedish Royal Academy of Sciences, Svenska Sällskapet för Antropologi och Geografi, Uppsala University Linné Fonden, and Sernanders Resestipendium for funding this work. We are especially grateful for the help and support of staff at Abisko Scientific Research Station and our field assistants (Pär Eriksson, Magnus Karlsson, Karin Luthbom, Marie Nilsson, Katrin Sjögersten and Per Thermaenius). We also thank Dr Benjamin Turner for help with the C, N and P analyses. Finally, two anonymous referees provided valuable suggestions and comments for improving this paper, and to them we also express our gratitude.

Appendix A

See Table A1.

References

Alexandersson, H., Karlstöm, C., Larsson-McCann, S., 1991. Temperaturen och Nederbörden i Sverige: 1961–1990 Referensnormaler. SMHI Meteorologi Report No. 81, SMHI (Sveriges meteorologiska och hydrologiska institut), Norrköping.

Anderson, J.M., 1991. The effects of climate change on decomposition processes in grassland and coniferous forests. Ecological Applications 1 (3), 326–347.

Ågren, G.I., 2000. Temperature dependence of old soil organic matter. Ambio 29 (1), 55.

Barnekow, L., Sandgren, P., 2001. Palaeoclimate and tree-line changes during the Holocene based on pollen and plant macrofossil records from six lakes at different altitudes in northern Sweden. Review of Paleobotany and Palynology 117, 109–118.

Bååth, E., Söderström, B., 1979. Fungal biomass and fungal immobilisation in Swedish coniferous forest soils. Revue d'Ecologie et de Biologie du Sol. 16, 477–489.

Batjes, N.H., Bridges, E.M., 1992. World inventory of soil emissions. International Soil Reference and Information Centre No. 92/4.

Bowden, R.D., Newkirk, K.M., Rullo, G.M., 1998. Carbon dioxide and methane fluxes by a forest soil under laboratory-controlled moisture and temperature conditions. Soil Biology & Biochemistry 30, 1591–1597.

Buchmann, N., 2000. Biotic and abiotic factors controlling soil respiration rates in *Picea abies* stands. Soil Biology & Biochemistry 32, 1625–1635.

Chapin, F.S. III, Reuss, R.W., 2001. The roots of the matter. Nature 411, 749–752.

Christensen, T.R., Jonasson, S., Callaghan, T.V., Havström, M., 1999. On the potential CO_2 release from tundra soil in a changing climate. Applied Soil Ecology 11, 127–134.

Dalias, P., Anderson, J.M., Bottner, P., Coûteaux, M.-M., 2001. Temperature responses of carbon mineralization in conifer forest soils from different regional climates incubated under standard laboratory conditions. Global Change Biology 6, 181–192.

Davidson, E.A., Belk, E., Boone, R.D., 1998. Soil water content and temperature as independent or confounded factors controlling soil

respiration in a temperate mixed hardwood forest. Global Change Biology 4, 217–227.

Dong, Y., Scharffe, D., Lobert, J.M., Crutzen, P.J., Sanhueza, E., 1998. Fluxes of CO_2 CH_4 and N_2O from a temperate forest soil: the effects of leaves and humus layers. Tellus 50B, 243–252.

Emanuel, W.R., Shugart, H.H., Stevenson, M.P., 1985. Climate change and broad-scale distribution of terrestrial ecosystem complexes. Climatic Change 7, 29–43.

Fang, C., Moncrieff, J.B., 2001. The dependence of soil CO_2 efflux on temperature. Soil Biology & Biochemistry 33, 155–165.

Flanagan, P.W., Veum, A.K., 1974. Relationship between respiration, weight loss, temperature, and moisture in organic residues on tundra. In: Holding, A.J., Heal, O.W., MacLean, S.F. Jr., Flanagan, P.W. (Eds.), Soil Organisms and Decomposition in Tundra, Tundra Biome Steering Committee, Stockholm, pp. 249–277.

Giardina, C.P., Ryan, M.G., 2000. Evidence that decomposition rates of organic carbon in mineral soil do not vary with temperature. Nature 404, 858–861.

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

Hobbie, S.E., Schimel, J.P., Trumbore, S.E., Randerson, J.R., 2000. Controls over carbon storage and turnover in high-latitude soils. Global Change Biology 6 (Suppl. 1), 196–210.

Hodkinson, I.D., Webb, N.R., Bale, J.S., Block, W., 1999. Hydrology, water availability and tundra ecosystem function in a changing climate: the need for a closer integration of ideas? Global Change Biology 5, 359–369.

Högberg, P., Nordgren, A., Buchmann, N., Taylor, A.F.S., Ekblad, A., Högberg, M.N., Nyberg, G., Ottosson-Löfvenius, M., Read, D.J., 2001. Large-scale forest girdling shows that current photosynthesis drives soil respiration. Nature 411, 789–792.

Holmgren, B., Tjus, M., 1996. Summer air temperatures and treeline dynamics at Abisko. Ecological Bulletins 45, 159–169.

Janssens, I.A., Lankreijer, H., Matteucci, G., Kowalski, A.S., Buchmann, N., Epron, D., Pilegaard, K., Kutsch, W., Longdoz, B., Grunwald, T., Montagnani, L., Dore, S., Rebmann, C., Moors, E.J., Grelle, A., Rannik, U., Morgenstern, K., Oltchev, S., Clement, R., Gudmundsson, J., Minerbi, S., Berbigier, P., Ibrom, A., Moncrieff, J., Aubinet, M., Bernhofer, C., Jensen, N.O., Vesala, T., Granier, A., Schulze, E.D., Lindroth, A., Dolman, A.J., Jarvis, P.G., Ceulemans, R., Valentini, R., 2001. Productivity overshadows temperature in determining soil and ecosystem respiration across European forests. Global Change Biology 7, 269–278.

Kampichler, C., Bruckner, A., Kandeler, E., 2001. Use of enclosed model ecosystems in soil ecology: a bias towards laboratory research. Soil-Biology & Biochemistry 33, 269–275.

Kittel, T.G.F., Steffen, W.L., Chapin, F.S. III, 2000. Global and regional modelling of Arctic-boreal vegetation distribution and its sensitivity to altered forcing. Global Change Biology 6, 1–18.

Körner, C., 1998. A re-assessment of high elevation treeline positions and their explanation. Oecologia 115, 445–459.

Liski, J., Ilvesniemi, H., Makela, A., Westman, C.J., 1999. CO_2 emissions from soil in response to climatic warming are overestimated—the decomposition of old soil organic matter is tolerant of temperature. Ambio 28, 171–174.

Lloyd, J., Taylor, J.A., 1994. On the temperature dependence of soil respiration. Functional Ecology 8, 315–323.

Londo, A.J., Messina, M.G., Schoenholtz, S.H., 1999. Forest harvesting effects on soil temperature, moisture, and respiration in a bottomland hardwood forest. Soil Science Society of America Journal 63, 637–644.

Nadelhoffer, K.J., Giblin, A.E., Shaver, G.R., Laundre, J.A., 1991. Effects of temperature and substrate quality on element minerlisation in six arctic soils. Ecology 72, 242–253.

Nakane, K., Khno, T., Horikoshi, T., Nakatsubo, T., 1997. Soil carbon cycling at a black spruce (*Picea mariana*) forest stand in Saskatchewan, Canada. Journal of Geophysical Research28,793.

Norby, R.J., Cotrufo, M.F., Ineson, P., O'Neill, E.G., Canadell, J.G., 2001. Elevated CO_2, litter chemistry, and decomposition: a synthesis. Oecologia 27, 153–165.

Oechel, W.C., Vourlitis, G.L., Hastings, S.J., Zulueta, R.C., Hinzman, L., Kane, D., 2000. Acclimation of ecosystem CO_2 exchange in the Alaskan Arctic in response to decadal climate warming. Nature 406, 978–981.

Overpeck, J., Hughen, K., Hardy, D., Bradley, R., Case, R., Douglas, M., Finney, B., Gajewski, K., Jacoby, G., Jennings, A., Lamoureux, S., Lasca, A., MacDonald, G., Moore, J., Retelle, M., Smith, S., Wolfe, A., Zielinski, G., 1997. Arctic environmental change of the last four centuries. Science 278, 1251–1256.

Panikov, N.S., 1997. A kinetic approach to microbial ecology in arctic and boreal ecosystems in relation to global change. In: Oechel, W.C., Callaghan, T., Gilmanov, T., Holten, J.I., Maxwell, B., Molau, U., Sveinbjörnsson, B. (Eds.), Global Change and Arctic Terrestrial Ecosystems, Springer, New York, pp. 171–188.

Peterjohn, W.T., Melillo, J.M., Steudler, P.A., Newkirk, K.M., 1994. Responses of trace gas fluxes and N availability to experimental elevated temperatures. Ecological Applications 4, 617–625.

Raich, J.W., Potter, C.S., 1995. Global patterns of carbon dioxide emissions from soils. Global Biogeochemical Cycles 9, 23–36.

Raich, J.W., Schlesinger, W.H., 1992. the global carbon doixide flux in soil respiration and its relationship to vegetation and climate. Tellus 44B, 81–91.

Raich, J.W., Tufekciouglu, A., 2000. Vegetation and soil respiration: correlation and controls. Biogeochemistry 48, 71–90.

Reichstein, M., Bednorz, F., Broll, G., Kåtterer, T., 2000. Temperature dependence of carbon mineralisation: conclusions from a long-term incubation of subalpine soil samples. Soil Biology & Biochemistry 32, 947–958.

Robinson, C.H., Wookey, P.A., 1997. Microbial ecology, decomposition and nutrient cycling. In: Woodin, S.J., Marquiss, M. (Eds.), The Ecology of Arctic Environments, Special Publication Number 13 of The British Ecological Society, Blackwell Science, Oxford, pp. 41–68.

Rustad, L.E., Campell, J.L., Marion, G.M., Norby, R.J., Mithcell, M.J., Hartley, A.E., Cornelissen, J.H.C., Gurevitch, GCTE-NEWS, 2001. A meta-analysis of the response of soil respiration net nitrogen mineralization, and aboveground plant growth to experimental ecosystem warming. Oecologia 126, 543–562.

Schleser, G.H., 1982. The response of CO_2 evolution from soils to global temperature changes. Zeitschrift für Naturforschung 37a, 287–291.

Schlesinger, W.H., 1997. Biogeochemistry, An Analysis of Global Change, 2nd ed., Academic Press, San Diego, CA, 588 pp.

Simmons, J.A., Fernandez, I.J., Briggs, R.D., Delaney, M.T., 1996. Forest floor carbon pools and fluxes along a regional climate gradient in Maine, USA. Forest Ecology and Management 84, 81–95.

Sjögersten, S., Turner, B.L., Mahieu, N., Condron, L.M., Wookey, P.A., 2002. Soil organic matter biochemistry and potential susceptibility to climatic change across the forest-tundra ecotone in the Fennoscandian mountains. Global Change Biology in press.

Smith, S.E., Read, D.J., 1997. Mycorrhizal Symbiosis, Academic Press, London.

StatSoft, 1995. STATISTICA Volume 1—General Conventions and Statistics I, 2nd ed., StatSoft, Tulsa.

Stötter, J., Wasti, M., Caseldine, C., Haberle, T., 1999. Holocene palaeoclimatic reconstruction in northern Iceland approaches and results. Quaternary Science Reviews 18, 457–474.

Swift, M.J., Heal, O.W., Andreson, J.M., 1979. Decomposition in terrestrial Ecosystems, Blackwell Science, Oxford.

Sylvia, D.M., Fuhrmann, J.J., Hartel, P.G., Zuberer, D.A., 1998. Principles and Application of Soil Microbioglogy, Prentice-Hall, New York.

Torn, M.S., Trumbore, S.E., Chadwick, O.A., Vitousek, P.M., Hendricks, D.M., 1997. Mineral control of soil organic carbon storage and turnover. Nature 389, 170–173.

Vance, E.D., Chapin, F.S. III, 2001. Substrate limitations to microbial activity in taiga forest floors. Soil Biology & Biochemistry 33, 173–188.

Vance, E.D., Brookes, P.C., Jenkinsons, D.S., 1987. An extraction method for measuring soil microbial biomass-C. Soil Biology & Biochemistry 19, 703–707.

White, A., Canell, M.G.R., Friend, A.D., 2000. The high-latitude terrestrial carbon sink: a model analysis. Global Change Biology 6, 227–245.

Widén, B., 2001. CO_2 exchange within a Swedish Coniferous forest spatial and temporal variation. Silvestria 184, Acta Universitatis Agriculturae Suecia.

Wütrich, C.H., Döbeli, C., Schaub, D., Leser, H., 1994. The pattern of carbon-minerlisation in the high Arctic tundra (western and northern Spitsbergen) as an expression of landscape ecologic environment heterogeneity. Zeitskrift für Geomorfologie 97 (Suppl.-Bd.), 251–264.