

Potential CO₂-production in aerobic conditions from a Siberian tundra environment

Manfred Bölder^{1*}, Wiebke Müller-Lupp¹, Kumiko Takata²,
Hironori Yabuki² and Rolf Möller¹

¹*Institute for Polar Ecology, Wischhofstr. 1–3 Bldg. 12, 24148 Kiel, Germany*

²*Frontier Research System for Global Change, Showa-machi,
Kanazawa-ku, Yokohama 236-0001*

Abstract: Soil respiration was analysed from different soil profiles of an arctic tundra environment (Samoylov Island, Lena Delta, East Siberia) during field studies in 1998 and 1999. Samples from discrete soil layers (0–47 cm), from the soil surface down to the permafrost table, were incubated and analysed for CO₂-evolution at different temperatures, related to ambient values (0°C to 20°C) in a dynamic chamber system. The soil investigated was located in a low-centre polygon on a poorly drained peat terrace and determined as a Glacial Aquiturbel.

Soil respiration data from the individual layers of this location were combined with soil temperature measurements of a comparable tundra environment near Tiksi. These data were split into discrete intervals of 5°C, which were regarded as intervals for different levels of soil microbial activity. Time spans for these temperature ranges were calculated and used as a base for further calculations of potential seasonal CO₂-emissions.

Changing patterns of soil respiration could be related to varying substrate conditions and effects of physical factors, especially freezing and thawing. They are regarded as important factors controlling CO₂-flux from tundra soils. High levels of CO₂-evolution can be attributed to soil layers where high amounts of organic matter are available, oxygen penetrates through soil pores and elevated temperatures above 0°C maintain metabolic processes.

key words: soil respiration, permafrost, arctic, active layer, tundra

Introduction

The Arctic tundra is an important storehouse of carbon; 90% to 98% of the total carbon of tundra ecosystems is located in these soils (Miller *et al.*, 1983). The Russian tundra comprises about 32% of world tundra systems (Zamolodchikov *et al.*, 1997) showing various types of landscapes and soils with specialised functionality (Alexandrova, 1988). Wet and cold conditions in Arctic soils lead to restricted decomposition of litter and therefore to the development of huge carbon stocks (Gorham, 1991). Recent discussions on the function of this system in the global carbon cycle indicate a change from a carbon sink to a carbon source (Billings *et al.*, 1983; Oechel *et al.*, 1993). Hence, tundra regions have become key regions for studies of global carbon fluxes.

*E-mail: mboelter@ipoe.uni-kiel.de

Soil respiration is the main driving for the metabolic process, which produces soil carbon turnover and CO₂-evolution, although above ground respiration alone can contribute significant amounts of CO₂ to the atmosphere (Oberbauer *et al.*, 1996). Soil respiration can mainly be divided into root and microbial respiration with respect to individual tundra environments (Dennis and Johnson, 1970; Billings *et al.*, 1977; Illeries and Jonasson, 1999). Several environmental and plant related factors control this process, such as water table shifts, oxygenation, temperature and litter quality (Flanagan, 1986; Christensen *et al.*, 1997; Grogan and Chapin, 1999; Scanlon and Moore, 2000). The pure diffusion process is modified by meteorological, hydrological and soil physical parameters, such as porosity or clay content.

Most studies of CO₂-efflux have been performed using enclosures and static procedures resulting in net CO₂-exchange rates from soil-plant-communities to the atmosphere (*e.g.*, Oechel and Billings, 1992; Vourlitis *et al.*, 1993). Many studies and compilations can be found with respect to seasonal aspects or different plant cover. Exclusive focus on the soil environment is less frequent, and analysis of individual depth layers has been performed only occasionally (Oechel *et al.*, 1997; Uchida *et al.*, 1998; Scanlon and Moore, 2000).

The main objective of this study was to determine potential soil respiration in different soil horizons in permafrost-affected soils (Lena Delta, East Siberia) with respect to CO₂-evolution related to temperature and other environmental effects. The analysis of long-term temperature readings offered insight into potential soil respiration over long periods.

Materials and methods

Site descriptions

Field studies of respiratory activity and soil science were conducted at Samoylov Island, East Siberia. Data for temperature records in soil profiles were performed at a site near Tiksi. These are study sites of two independent projects in Siberia (the *Russian-German Co-operation: Laptev Sea System* and the *Russian-Japanese Project GAME (GEWEX Asian Monsoon Experiment)-Siberia*).

1. Samoylov Island

Field studies of soil science and soil biology were carried out on Samoylov Island in the Lena Delta, East Siberia, during summer months of 1998 and 1999. This island is located in one of the main river channels (Olenyok Channel) in the southern part of the delta (N 72°, E 126°, Fig. 1). Samoylov Island has a size of about 1200 ha and can be regarded as representative of the south-western part of the Lena Delta, which consists of *ca.* 1500 islands. The island shows two geomorphologic patterns, an erosion area in the eastern part and an accumulation area in the western part. Abrasion and erosion have formed cliffs in the eastern parts up to 8 m high, and narrow beaches. Changing river water levels are responsible for periods of abrasion and accumulation of sediments. Results are strongly stratified soils. Their texture is dominated by sand; coarser fractions are missing, which prevents stronger frost sorting.

The age of the oldest parts with huge turf accumulation is estimated to be between

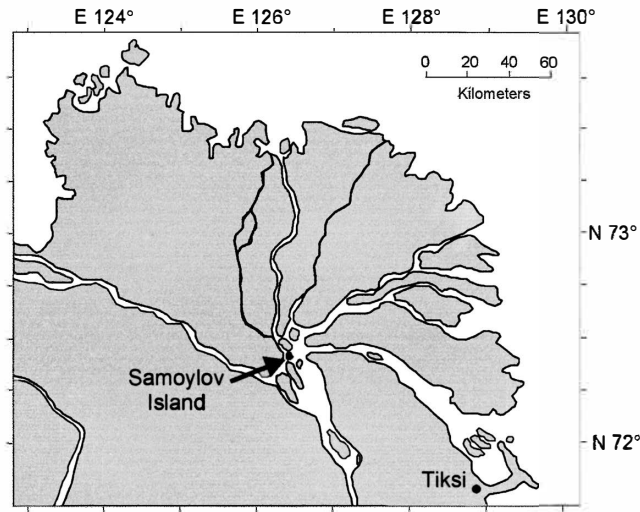


Fig. 1. Overview of the Lena-Delta, East Siberia. The investigation area, Samoylov Island, is marked by an arrow.

8000 and 9000 years (Grigoriev, 1983). This part of the island is dominated by polygon structures (low-centre polygons). The hydrological situation shows restricted drainage of the shallow active layer (20–80 cm). Low winter temperature (down to -40°C) and a thin snow cover, which is due to strong winds, support frost cracking (thermal contraction cracking), which results in polygonal patterned grounds interspersed with ice-wedges. Ice-rich permafrost is typical for the whole island. The depth of the active layer (30–80 cm) depends on vegetation cover, exposure, substrate, soil temperature and soil water content. Figures 2 and 3 show the local environment and a profile of the investigated plot, a trough of polygon structure.

Samplings for soil characteristics were carried out at the end of July 1998; soil respiration measurements were performed during summer 1999. Samplings for gas exchange measurements were performed by using metal cylinders of about 50 ml. Samples were placed into plastic containers and stored under ambient conditions until final measurements. The parent material of the ice-wedge polygon is poorly drained peat. The classification according to U.S. SOIL TAXONOMY (Soil Survey Staff, 1998) leads to Glacic Aquiturbel (Kutzbach, 2000). Maximum thaw depth at the end of the field season 1998 (Aug. 29) was 20 cm in the polygon centre and 37 cm in the apex area. Total pore volume was determined in the centre 56%, in the apex between 47 and 53 Vol.-%. Soil water contents were between 40 and 37 Vol.-% in the upper soil horizons, in deeper layers up to 49 Vol.-%. Soil bulk density reached values of 0.9 g cm^{-3} in the upper soil horizon and 1.4 g cm^{-3} deeper in the profile ($>10\text{ cm}$). Sand was the dominant fraction in all depths. Silt content was highest (31.6%) in the deepest layer (15–19 cm) and varied between 3.7 and 21.9% at other soil depths. Clay content was also highest in the layer near the permafrost table but did not exceed 6.2% (Müller-Lupp, 2002).



Fig. 2. Landscape of Samoylov Island.



Fig. 3. Investigation site at the edge of a low-centre polygon.

2. Tiksi

Field studies of the surface water and energy balance have been carried out since October 1997 at Tiksi (Kodama, 2000) in the low plains in this experimental watershed. Temperature records exist for 6 depths within the active layer at 0, 5, 10, 20, 30, and 48 cm. They are available in hourly intervals between September 1997 and August 1999.

The topography of the watershed consists of rolling hills with elevations of 200–300 m and gently sloping valleys (Fig. 4). Bottoms of the valleys form marshy wetlands (Watanabe *et al.*, 2001). Thaw depth depends on surface micro-undulation

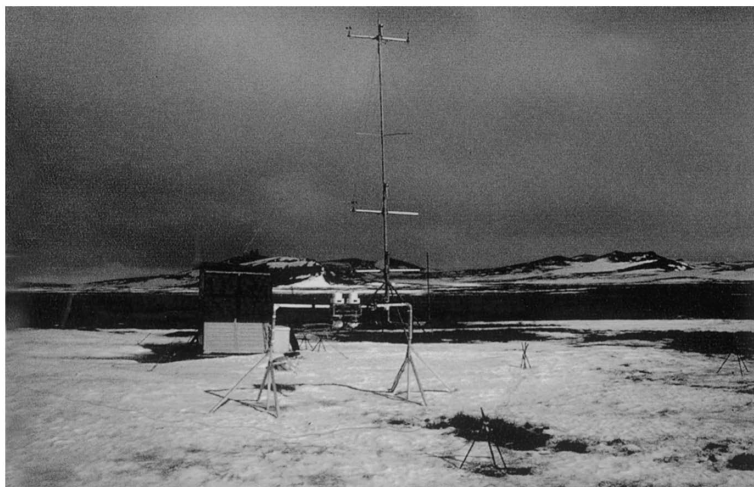


Fig. 4. Landscape near Tiksi showing the weather station of the GAME project.



Fig. 5. Soil profile at Tiksi, near weather station (Photo: K. Watanabe).

and vegetation cover. Shallow water tables are normal near the bottoms of the valleys. Relatively dry soils are present at hill slopes.

Sedges covered the sites where ground water level is low or the ground is inundated while mosses covered sites where the ground water level is a few centimetres below the soil surface (Watanabe and Mizoguchi, 1998; Watanabe *et al.*, 2000). The upper horizon contains many roots and much decomposed organic matter (Fig. 5). Lower horizons generally consist of clayey silt. Thaw depth at the end of August 1997 was 39 cm. The soil in the wetlands is a multi-layered system that consists of 0–20 cm of live

and accumulated organic material on 5–30 cm of partially decomposed organic matter, over mineral silt above the permafrost bedrock (Watanabe *et al.*, 2001). The hills are covered by mudstone with some lichens. Tundra polygons and frost boils are found in this area. Bulk density is 0.7 g cm⁻³ (range: 0.5–1.0) in the upper layers and 1.32 g cm⁻³ (range: 1.1–1.7) in the lower layers. Volumetric soil moisture is about 72% (range: 60–85%) in the upper, 52% (range: 40–65%) in the intermediate layer, and about 37% (range: 40–58%) in the lower. The high water contents of the upper layers are due to the occurrence of living moss, while the intermediate layer corresponds to the organic layers used for soil respiration measurements at Samoylov.

Soil respiration measurements

Soil respiration was measured in the field with a dynamic CO₂ gas exchange analysis system (Walz Company, Effeltrich, Germany). The CO₂-analyser (Binos, Rosemount, Germany) consists of an absolute CO₂-channel (0–2500 ppm) and a differential CO₂-channel (–50 ppm to +50 ppm). Measurements were carried out in a minicuvette, volume *ca.* 800 cm³, at flow of 500–1000 ml min⁻¹ (for details see Müller-Lupp, 2002), this is normal atmospheric air. About 25 cm³ of soil was incubated in the dark chamber. A stable CO₂-signal was reached after about 20 min and incubations then lasted for another 30 min. Measurements were carried out at temperatures from close to 0°C to +20°C due to ambient temperature from discrete soil layers. Samples from individual soil horizons (0–5 cm, 5–10 cm, 10–20 cm, 20–30 cm, 30–40 cm, 40–48 cm) were incubated.

Predictions of potential soil respiration are based on these respiration data (Table 1, 2: profile A) and on temperature data from the GAME-Siberia Project (Table 1). For calculations of potential soil respiration, temperature data are split into discrete intervals (–5~0°C, 0–5°C, 5–10°C, 10–15°C, and >15°C). We assumed that respiration takes place to temperatures down to –5°C, which can be accepted as a threshold for relevant metabolic processes (Coxson and Parkinson, 1987; Clein and Schimel, 1995). Time spans for these temperature ranges are calculated for each month (Table 1, section “temperature conditions”). These time spans are multiplied by corresponding CO₂-evolutions to yield potential CO₂-evolution data per month and gram soil (Table 1, section “potential CO₂-production”, [$\mu\text{g CO}_2 \text{ month}^{-1}\text{g}^{-1}$]). Subsequent multiplication by layer specific bulk density and summing up over all temperature ranges results in CO₂-evolution per month and volume (Table 1, section “potential CO₂-production”, [$\text{mg CO}_2 \text{ month}^{-1}\text{cm}^{-3}$]) for each specified layer. By integrating these potential CO₂-evolution rates over layer thickness, results give layer specific CO₂-respiration per month and unit area (Table 1, section “potential CO₂-production”, [$\text{mg CO}_2 \text{ month}^{-1} \text{cm}^{-2}$]). Conversion of the latter results into [$\text{g CO}_2 \text{ d}^{-1}\text{m}^{-2}$] gives potential mean daily CO₂-production with respect to specified months.

Results

A survey of air (2 m height) and soil temperature (here reduced to three depths) is given in Fig. 6.

In March 1998 air temperature was below –30°C and corresponding soil tem-

Table 1. Example for calculating area-related potential CO₂-efflux from gas exchange data, temperatures and soil related constraints.

layer	gas exchange measurements			temperature conditions		potential CO ₂ -emission in aspect of a specified month					
	temperature	CO ₂ -emission	C-org	temperature range	number of hours with temperature in range	CO ₂ -emission per g	bulk density	CO ₂ -emission per cm ³	layer thickness	CO ₂ -emission per unit area	mean daily CO ₂ -emission according to specified month
[cm]	[°C]	[µg CO ₂ / h / g]	[% _{d.wt.}]	[°C]	[h / month]	[µg CO ₂ / month / g]	[g / cm ³]	[mg CO ₂ / month / cm ³]	[cm]	[mg CO ₂ / month / cm ²]	[g CO ₂ / d / m ²]
0 - 5	0	6.68	31.70	-5 - 0	352	2351	0.9	7.4	5	37.0	12.3
	5	14.20		0 - 5	288	4090	0.9				
	10	20.65		5 - 10	69	1425	0.9				
	15	33.05		>10	11	364	0.9				
5 - 10	0	7.39	7.37	-5 - 0	288	2128	1.26	7.5	5	37.5	12.5
	5	8.80		0 - 5	423	3722	1.26				
	10	10.91		5 - 10	9	98	1.26				
	15	18.66		>10	0	0	1.26				
10 - 20	0	6.06	3.75	-5 - 0	187	1133	1.32	6.4	10	63.7	21.2
	5	6.93		0 - 5	533	3694	1.32				
	10	10.40		5 - 10	0	0	1.32				
	15	17.33		>10	0	0	1.32				
20 - 30	0	8.36	4.43	-5 - 0	0	0	1.32	8.9	10	89.0	29.7
	5	9.36		0 - 5	720	6739	1.32				
	10	13.37		5 - 10	0	0	1.32				
	15	18.38		>10	0	0	1.32				
30 - 40	0	6.66	5.71	-5 - 0	131	872	1.34	5.4	10	54.3	18.1
	5	5.39		0 - 5	589	3177	1.34				
	10	11.74		5 - 10	0	0	1.34				
	15	21.58		>10	0	0	1.34				
40 - 48	0	18.68	5.38	-5 - 0	451	8425	1.41	20.3	8	162.6	54.2
	5	22.28		0 - 5	269	5994	1.41				
	10	29.16		5 - 10	0	0	1.41				
	15	38.99		>10	0	0	1.41				

Table 2. CO₂-evolution rates ($\mu\text{g CO}_2 \text{ g}^{-1} \text{ h}^{-1}$), Q₁₀ values (0–10°C and 5–15°C) and water contents (w.c., % of w.wt) of two soil profiles with different plant cover of site 3 (Aug. 9, 1999).
A: polygon apex (cf. Fig. 3), B: polygon centre with a dense cover of mosses.

Profile	depth	w.c.	Temperature				Q ₁₀	
			0°C	5°C	10°C	15°C	0-10°C	5-15°C
A	0-5	57.6	6.7	14.2	20.7	33.0	3.1	2.3
	5-10	25.3	7.4	8.8	10.9	18.7	1.5	2.1
	10-20	33.0	6.1	6.9	10.4	17.3	1.7	2.5
	20-30	37.8	8.4	9.4	13.4	18.4	1.6	2.0
	30-40	43.0	6.7	5.4	11.7	21.6	1.8	4.0
	40-48	41.7	18.7	22.3	29.2	39.0	1.6	1.8
	48-50	36.9	13.3	15.7	20.4	29.4	1.5	1.9
B	0-5	285.0	31.3	39.7	75.2	133.6	2.4	3.4
	5-10	245.6	13.3	24.7	64.7	81.8	4.9	3.5
	10-15	324.5	18.4	21.7	51.7	103.5	2.8	4.8
	15-20	63.6	4.6	7.6	10.1	22.8	2.2	3.0
	20-25	38.4	8.8	9.7	16.5	21.5	1.9	2.1

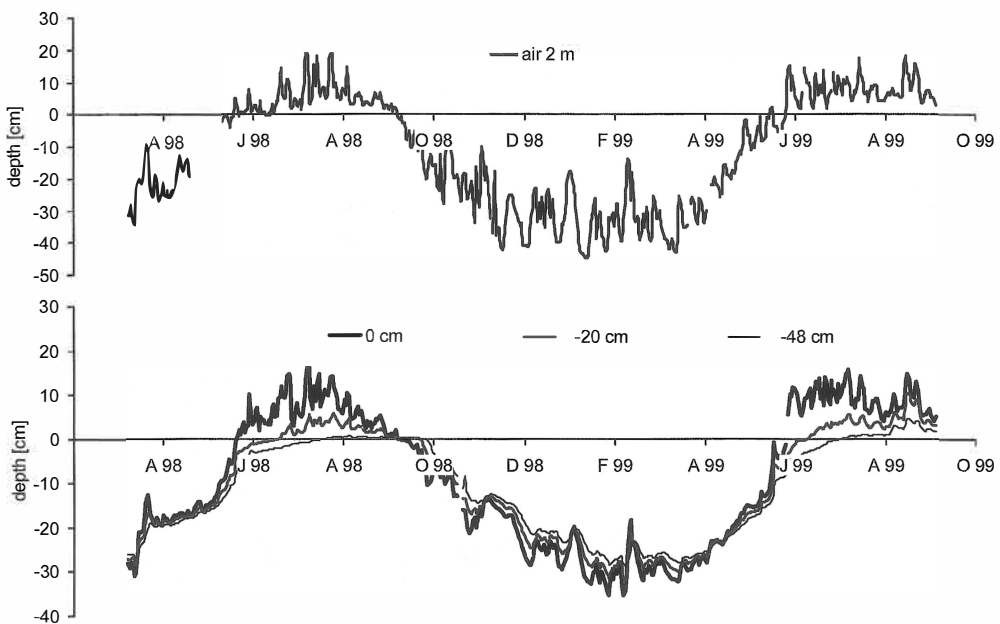


Fig. 6. Air and soil temperature at Tiksi (data source for air temperature: DWD, Germany).

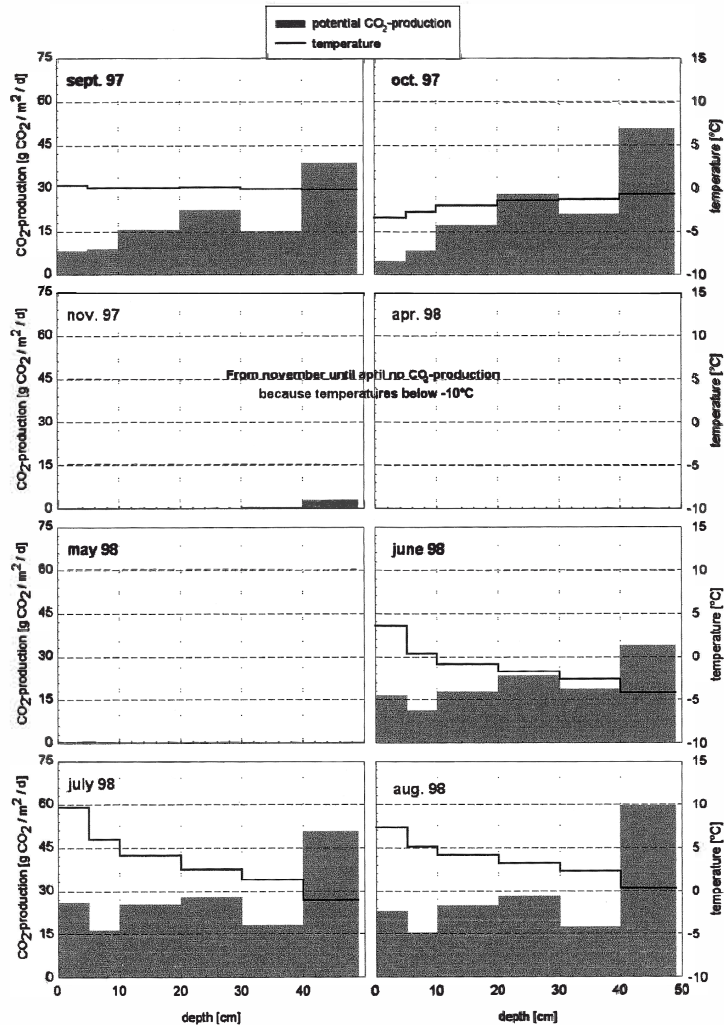


Fig. 7. Data for potential CO₂-production in depth layers and related temperatures.

peratures between the soil surface and 48 cm reached values around -25°C . An increase to positive values took place at the end of May; temperature remained positive, with maxima around 15°C , until freezing started at the end of September. Negative temperatures lasted for about 9 months until thawing started again in May 1999. Minimum winter air temperature was -45°C and minimum soil surface temperature was -35°C at 48 cm depth.

Table 2 shows the records of CO₂-evolution measured for 4 temperatures in late summer and related Q_{10} -values. An increase of CO₂-evolution concomitant to increasing temperature could be observed for all soil depths. It becomes evident for profile A that all incubation temperatures yield high CO₂ at the deepest horizons, sometimes even higher than those of the top layers. Related Q_{10} -values keep a constant pattern with

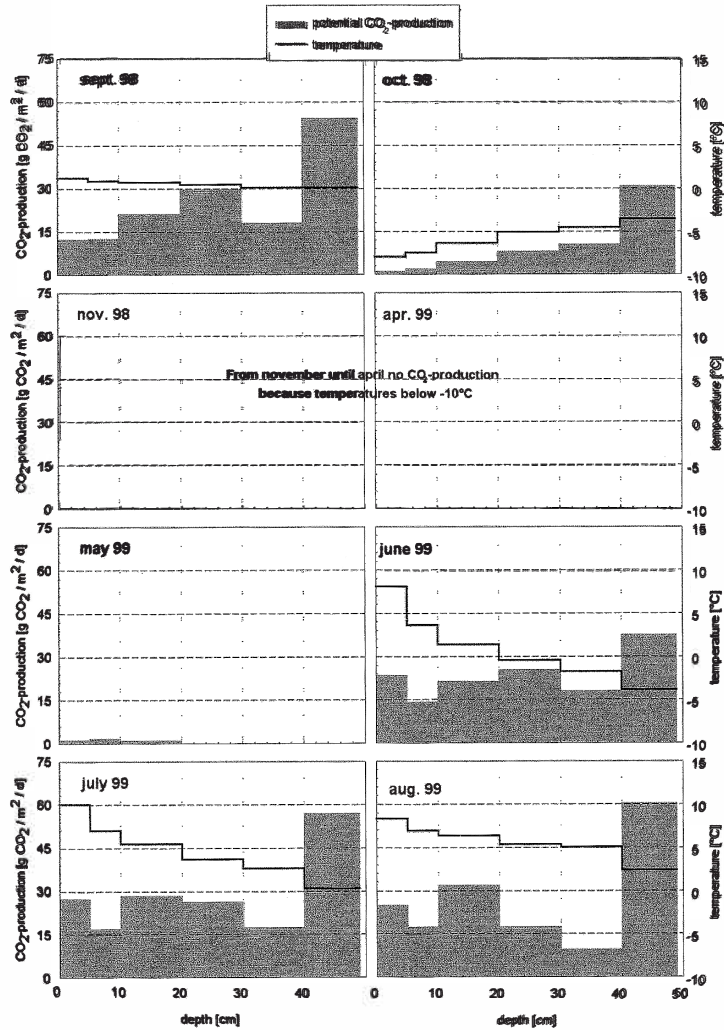


Fig. 7. Continued.

only a few exceptions. The profile with denser moss plant cover (B) shows a clear decreasing trend with depth. Similar trends with elevated CO₂-evolution rates next to the permafrost table were observed also for other depth profiles, which were sampled and analysed for even more depth layers.

Further, it becomes evident that individual soil layers show very individual reactions to increasing temperatures. The lowest level in profile A was sampled at the permafrost table while the soil was frozen. From this it can be seen that the permafrost table reacts as a barrier for water, which has been percolated through the soil and obviously, has transported nutrients to these levels. Concomitant investigations of bacteria (Schulz, 1999) also show an increase in their abundance by elevated numbers and biomass. The pronounced decrease in profile B below 15 cm can be attributed to

Table 3. Accumulated CO₂-production for months September 1997–August 1999.

Month	Potential CO ₂ -emission per day and layer					
	0 - 5 cm	0 - 10 cm	0 - 20 cm	0 - 30 cm	0 - 40 cm	0 - 48 cm
	[g CO ₂ m ⁻² layer ⁻¹ d ⁻¹]					
Sep 97	8.4	17.4	32.9	55.4	70.7	109.2
Oct 97	4.7	13.1	30.3	58.5	79.6	130.2
Nov 97	0.0	0.0	0.0	0.1	0.5	3.5
Dec 97	0.0	0.0	0.0	0.0	0.0	0.0
Jan 98	0.0	0.0	0.0	0.0	0.0	0.0
Feb 98	0.0	0.0	0.0	0.0	0.0	0.0
Mar 98	0.0	0.0	0.0	0.0	0.0	0.0
Apr 98	0.0	0.0	0.0	0.0	0.0	0.0
Mai 98	0.3	0.3	0.3	0.3	0.3	0.3
Jun 98	16.5	27.9	45.7	69.1	87.8	121.4
Jul 98	26.1	42.4	68.0	95.7	113.8	164.3
Aug 98	22.9	38.2	63.3	91.2	108.6	168.0
Sep 98	12.3	24.8	46.1	75.7	93.8	148.0
Oct 98	1.1	3.0	7.5	15.7	26.1	56.9
Nov 98	0.0	0.0	0.0	0.0	0.0	0.0
Dec 98	0.0	0.0	0.0	0.0	0.0	0.0
Jan 99	0.0	0.0	0.0	0.0	0.0	0.0
Feb 99	0.0	0.0	0.0	0.0	0.0	0.0
Mar 99	0.0	0.0	0.0	0.0	0.0	0.0
Apr 99	0.0	0.0	0.0	0.0	0.0	0.0
Mai 99	1.3	3.0	4.2	4.2	4.2	4.2
Jun 99	23.5	37.6	59.0	84.4	102.5	140.0
Jul 99	27.4	44.4	72.7	99.0	116.4	173.3
Aug 99	25.0	42.4	74.3	91.6	101.2	161.5

drastically lower organic matter content. Table 2 also shows a much differentiated pattern of Q₁₀-values. There is no direct relationship to depth but elevated mean values for the temperature span 5–15°C versus 0–10°C can be observed for both soil profiles.

Data of profile A have been used to extrapolate soil respiration for seasonal patterns. Figure 7 shows the results for mean potentially respired amounts of CO₂ for each month. Due to the elevated levels of potential CO₂-production in the deep horizons and the long persistence of temperatures above –5°C, which allows an active metabolism, these soil layers show the highest potential contributions of CO₂ in relation to the total profile. These production rates of CO₂ can even last for longer times in deep layers than in the top horizons. They are frozen much earlier in the year than the deep layers. Table 3 gives an overview of the potential CO₂-production, which has accumulated for the depth layers. From this table, it becomes possible to figure out the depths, which actually might be in direct exchange with the atmosphere. However, it can be seen that the deep soil layers need special attention.

Discussion

Permafrost affected soils of Siberia, mostly tundra environments, have been study sites for carbon balances since the IBP studies. Tundras have been regarded as

important carbon accumulation areas with rates of more than 100 gCm⁻²y⁻¹ (Whittaker, 1975; Billings *et al.*, 1982). Studies on degrading permafrost (Osterkamp and Romanovsky, 1996) show significant changes in these environments, which affect on soils and soil biological patterns (Bölter, 1996; Stonehouse, 1999). Long-term shifts of temperatures in soil horizons, which can be suspected to be involved in CO₂-evolution thus become of special interest. This holds especially true for gas evolutions during the cold seasons and below snow cover. Reports from Siberian and Alaskan tundra, and various alpine regions, have shown the significance of winter CO₂-efflux (Zimov *et al.*, 1993, 1996; Sommerfeld *et al.*, 1993; Mariko *et al.*, 1994; Oechel *et al.*, 1997). The studies at IBP sites have further shown that significant amounts of litter are decomposed during winter (Coyne and Kelley, 1978).

Thus, there is much evidence for microbial activity in the tundra environment even at temperatures below -5°C (Flanagan and Bunnell, 1980; Zimov *et al.*, 1993; Rivkina *et al.*, 2000). The activity, however, is at only low levels, with respect to CO₂-evolution, and recovers to optimal rates at much higher temperature (Bölter, 1991). Nevertheless, long periods of low CO₂-production can build up high concentrations of CO₂ in those soils or below snow cover. Mariko *et al.* (2000) measured a linear gradient under snow and found at 100 cm depth a CO₂-concentration of 1.4 ml l⁻¹. Oechel *et al.* (1997) also report CO₂-production rates in a tundra environment in relation to a depth gradient and show high rates at even great soil depth.

The process, which allows the CO₂ to reach the atmosphere from deep soil horizons, is still a matter of speculation. There are barriers: the frozen topsoil and the snow package. High amounts of potential CO₂-production in autumn (September and October, Fig. 7) can find a way to the surface as the soil is not completely frozen, since the seasonal mean temperature in the surface layer does not go far below -5°C. Zimov *et al.* (1996) and Oechel *et al.* (1997) report that this season shows the highest CO₂-effluxes. The very low soil temperatures from November to May, however, do not allow active CO₂-production from the respiration process, and the figures in November 1997 (Fig. 7) seem to be negligible. A possible source for elevated spring and autumn CO₂-release may be the phase change from water to ice (Coyne and Kelley, 1971).

The very large amounts of CO₂, which *can* be produced in deep layers—also during summer and spring—cannot be regarded as actual rates and need to be discussed as potential rates. Reasons for such high measurements (Table 3, Fig. 7) may be mechanical disturbances of the original soil layer and especially the fresh support of oxygen during the measurements in the flow chamber. Nevertheless, there are some reasonable indications, which support these data. On the one hand, we found an increasing amount of bacteria close to the permafrost table (Schulz, 1999); on the other hand, there were extreme high values of dissolved CO₂ in the pore water (Pfeiffer and Wagner, AWI Potsdam, pers. commun.). Hence, there are three independent hints, which refer to significant microbial activity in these layers.

The carbon source for such activity, however, cannot be explained fully. It is known that cryptogams release high amounts of sugars and sugar alcohols into the environment (Tearle, 1987; Melick and Seppelt, 1992, 1994). These carbohydrates and polyols are not used immediately but successively (Melick *et al.*, 1994), which allows for their transport to deeper layers—and accumulation and storage for later use. Unfortu-

nately, there are no data available on dissolved carbohydrates for these environments—there is an urgent need for further research on the carbon balances.

Our data on CO₂-evolution of the surface horizons (0–10 cm) match well to other studies performed in tundra regions. However, integrations to area related data of potential CO₂-evolution by using the data of the individual horizons results in values, which exaggerate data from other sources. Several points have, therefore, to be kept in mind, as to what may cause such high values and try to explain the mismatches:

- a) not the full active layer produces CO₂ “as much as it can”, but acts at lowered levels,
- b) the CO₂ does not reach the surface because of hampered diffusion,
- c) reduced oxygen partial pressure, enrichment of CO₂, and low levels of available carbohydrates,
- d) large amounts of CO₂ are re-used by the plant cover during photosynthesis.

Table 3 shows which layer—*i.e.*, the produced CO₂—might be in exchange with the atmosphere. By using the accumulated CO₂-values and going into the soil profile, it becomes possible to compare these data with those in the literature. We further have to take into consideration that much of the CO₂ which is produced in the soil can be reused directly by the plant cover. Sommerkorn (1998) estimated such reuse of CO₂ from soil respiration by mosses to be in the range from 35% to more than 90%.

On the other hand, the depth related estimated CO₂ production (Table 3) can be compared with the net carbon assimilation rate, which is regarded to balance the soil respiration by assuming the net ecosystem productivity to be equilibrated (Takata *et al.*, 2001). They calculated the net carbon assimilation rate with a land surface hydrological model, MATSIRO (Takata, pers. commun.), which includes the energy and water balance at the land surface and the photosynthetic processes of tundra vegetation. The input data of MATSIRO were the meteorological observation data of GAME-Siberia near Tiksi, and the calculated net carbon assimilation rate was 5.8 g CO₂ d⁻¹ m⁻². That is about half of the CO₂-production from 0–5 cm soil (Table 3).

All these points have to be taken into account when dealing with CO₂-evolution data from tundra environments. Further, the strong patchiness in terms of plant cover, soil structure, water and nutrient availability or support by local effects, *e.g.*, relief, has to be regarded carefully when approaches of measurements in limited methodological frames are performed. Their results have to be restricted to the region and season where/when they are taken. This model presented here is one approach to elucidate possible constraints for soil respiration in tundra environments.

Acknowledgments

We are greatly indebted to the Alfred-Wegener-Institute for Polar and Marine Research for logistic support. Many thanks go to our colleagues who spent with us the field seasons 1998 and 1999. The German Ministry of Science provided financial support for the studies at Samoylov Island for Science and Technology (Grant BMBF 03G0534). The studies at Tiksi were carried out as a part of GAME (GEWEX Asia Monsoon Experiment)-Siberia.

References

- Aleksandrova, V.D. (1988): Vegetation of the Soviet Polar Deserts. Cambridge, Cambridge University Press, 228 p.
- Billings, W.D., Peterson, K.M. and Shaver, G.R. (1977): Effect of temperature on root growth and respiration in a tundra ecosystem, Barrow, Alaska. The Below Ground Ecosystem: A Synthesis of Plant-Associated Processes, ed. by J.K. Marshall. Fort Collins, Colorado State University, 111–116 (Range Science Dept. Sci. Series No. 26).
- Billings, W.D., Luken, J.O., Mortensen, D.A. and Peterson, K.M. (1982): Arctic tundra: A source or sink for atmospheric carbon dioxide in a changing environment? *Oecologia*, **53**, 7–11.
- Billings, W.D., Luken, J.O., Mortensen, D.A. and Peterson, K.M. (1983): Increasing atmospheric carbon dioxide: possible effects on arctic tundra. *Oecologia*, **58**, 286–289.
- Bölter, M. (1991): Microbial mineralization in soils and on plant material from Antarctica. International conference on the role of the polar regions. Global Change: Proceedings of a conference held June 11–15, 1990 at the University of Alaska Fairbanks, ed. by G. Weller *et al.* Geophys. Inst. Univ. Alaska Fairbanks, Vol. II, 418–422.
- Bölter, M. (1996): Consequences of global warming on soil processes in Arctic regions. *Polarforschung*, **66**, 1–10.
- Christensen, T.R., Michelsen, A., Jonasson, S. and Schmidt, I.K. (1997): Carbon dioxide and methane exchange of a subarctic heath in response to climate change related environmental manipulations. *Oikos*, **79**, 34–44.
- Clein, J.S. and Schimel, J.P. (1995): Microbial activity of tundra and taiga soils at sub-zero temperatures. *Soil Biol. Biochem.*, **27**, 1231–1234.
- Coxson, D.S. and Parkinson, D. (1987): Winter respiratory activity in aspen woodland forest floor litter and soils. *Soil Biol. Biochem.*, **19**, 49–59.
- Coyne, P.I. and Kelley, J.J. (1971): Release of carbon dioxide from frozen soil to the Arctic atmosphere. *Nature*, **234**, 407–408.
- Coyne, P.I. and Kelley, J.J. (1978): Meteorological assessment of CO₂ exchange over an Alaskan Arctic tundra. Vegetation and Production Ecology of an Alaskan Arctic Tundra, ed. by L. Tieszen. Berlin, Springer-Verlag, 299–321 (*Ecol. Stud.* 29).
- Dennis, J.G. and Johnson, P.L. (1970): Shoot and rhizome standing crops of tundra vegetation at Barrow, Alaska. *Arct. Alp. Res.*, **2**, 253–266.
- Flanagan, P.W. (1986): Substrate quality influences on microbial activity and mineral availability in taiga forest floors. Forest Ecosystems in the Alaskan Taiga, ed. by K. Van Cleve *et al.* New York, Springer-Verlag, 138–151 (*Ecol. Stud.* 57).
- Flanagan, P.W. and Bunnell, F.L. (1980): Microflora activities and decomposition. An Arctic Ecosystem: the Coastal Tundra at Barrow, Alaska, ed. by J. Brown *et al.* Stroudsburg, Pennsylvania, Dowden, Hutchinson and Ross, 291–334.
- Gorham, E. (1991): Northern peatlands: Role in the carbon cycle and probable response to climate warming. *Ecol. Appl.*, **1**, 182–195.
- Grigoriev, M.N. (1983): Cryomorphogenesis in the Lena Delta. Yakutsk, Permafrost Institute Press.
- Grogan, P. and Chapin, F.S. III (1999): Arctic soil respiration: effects of climate and vegetation depend on season. *Ecosystems*, **2**, 451–459.
- Illeries, L. and Jonasson, S. (1999): Soil and plant CO₂ emission in response to variations in soil moisture and temperature and to amendment with nitrogen, phosphorus, and carbon in northern Scandinavia. *Arct. Antarct. Alp. Res.*, **32**, 264–271.
- Kodama, Y. (2000): The outline of the field observations in Tundra region in 1999. Activity Report of GAME-Siberia 1999. *GAME Publ.*, **21**, 7–14.
- Kutzbach, L. (2000): Die Bedeutung der Vegetation und bodeneigener Parameter für die Methanflüsse in Permafrostböden. Unpubl. Diplom Thesis, Inst f. Soil Science, Univ. Hamburg, 105 p.
- Mariko, S., Bekku, Y. and Koizumi, H. (1994): Efflux of carbon dioxide from snow-covered forest soils. *Ecol. Res.*, **9**, 343–350.
- Mariko, S., Nishimura, N., Mo, W., Matsui, Y., Kibe, T. and Koizumi, H. (2000): Winter CO₂ flux from snow

- surfaces in a cool-temperate deciduous forest, Japan. *Ecol. Res.*, **15**, 363–372.
- Melick, D.R. and Seppelt, R.D. (1992): Loss of soluble carbohydrates and changes in freezing points of Antarctic bryophytes after leaching and repeated freeze-thaw cycles. *Antarct. Sci.*, **4**, 399–404.
- Melick, D.R. and Seppelt, R.D. (1994): Seasonal investigations of soluble carbohydrates and pigment levels in Antarctic bryophytes and lichens. *The Bryologist*, **97**, 13–19.
- Melick, D.R., Bölter, M. and Möller, R. (1994): Rates of soluble carbohydrate utilization in soils from the Windmill Islands Oasis, Wilkes Land, continental Antarctica. *Polar Biol*, **14**, 59–64.
- Miller, P.C., Kendall, R. and Oechel, W.C. (1983): Simulating carbon accumulation in northern ecosystems. *Simulation*, **40**, 119–131.
- Müller-Lupp, W. (2002): Gefrier- und Tauprozesse im sibirischen Permafrost—Untersuchungs-methoden und ökologische Bedeutung. *Ber. Polarforsch.*, **415**, 1–145.
- Oberbauer, S.F., Gillespie, C.T., Cheng, W., Sala, A., Gebauer, R. and Tenhunen, J.D. (1996): Diurnal and seasonal patterns of ecosystem CO₂ flux from upland tundra in the foothills of the Brooks Range, Alaska, U.S.A. *Oecologia*, **125**, 512–520.
- Oechel, W.C. (1993): Understanding the impact of climatic change on northern ecosystems. *Impacts of Climate Change on Natural Ecosystems with Emphasis on Boreal and Arctic/Alpine Areas*, ed. by J.I. Holten *et al.* Trondheim, Norwegian Institute for Nature Research, 5–7.
- Oechel, W.C. and Billings, W.D. (1992): Effects of global change on the carbon balance of arctic plants and ecosystems. *Physiological Ecology of Arctic Plants: Implications for Climate Change*, ed. by F.S. Chapin *et al.* New York, Academic Press, 139–168.
- Oechel, W.C., Callaghan, T.V., Gilmanov, T., Holten, J.I., Maxwell, B., Molau, U. and Sveinbjörnsson, B., ed. (1997): *Global Change and Arctic Terrestrial Ecosystems*, New York, Springer, 493 p.
- Osterkamp T.E. and Romanovsky, V.E. (1996): Characteristics of changing permafrost temperatures in the Alaskan Arctic, U.S.A. *Arct. Alp. Res.*, **28**, 267–273.
- Rivkina, E.M., Friedmann, E.I., McKay, C.P. and Gilichinsky, D.A. (2000): Metabolic activity of permafrost bacteria below the freezing point. *Appl. Environ. Microbiol.*, **66**, 3230–3233.
- Scanlon, D. and Moore, T. (2000): Carbon dioxide production from peatland soil profiles: the influence of temperature, oxic/anoxic conditions and substrate. *Soil Sci.*, **165**, 153–160.
- Schulz, B. (1999): Bodenmikrobiologische Untersuchungen an einem Low-Center-Polygon im Lena-Delta. Unpubl. Diplom Thesis, Inst. f. Soil Science, Univ. Kiel, 59 p.
- Soil Survey Staff (1998): *Keys to soil taxonomy*. U.S. Dept. Agric. Nat. Res. Conserv. Serv., Washington D. C., 8th ed.
- Sommerfeld, R.A., Mosier, A.R. and Musselman, R.C. (1993): CO₂, CH₄ and N₂O flux through a Wyoming snowpack and implications for global budgets. *Nature*, **361**, 140–142.
- Sommerkorn, M. (1998): Patterns and controls of CO₂ fluxes in wet tundra types of the Taimyr Peninsula, Siberia—the contribution of soils and mosses. *Ber. Polarforsch.*, **98**, 1–219.
- Stonehouse, B. (1999): Biological processes in cold soils. *Polar Rec.*, **35**, 5–10.
- Takata, K., Yabuki, H., Sato, T., Bölter, M., Emori, S., Kodama, Y. and Ohata, T. (2001): Surface energy/water balance in the tundra region estimated by a one-dimensional land surface model—An examination of transpiration by CO₂ flux—. *Proceedings of the Fifth International Study Conference on GEWEX in Asia and GAME*, GAME Publ., No. **31**, 30–35.
- Tearle, P.V. (1987): Cryptogamic carbohydrate release and microbial response during freeze-thaw cycles in Antarctic fellfield fines. *Soil Biol. Biochem.*, **19**, 381–390.
- Uchida, M., Nakatsubo, T., Horikoshi, T. and Nakane, K. (1998): Contribution of micro-organisms to the carbon dynamics in black spruce (*Picea mariana*) forest soil in Canada. *Ecol. Res.*, **13**, 17–26.
- Vourlitis, G.L., Oechel, W.C., Hastings, S.J. and Jenkins, M.A. (1993): The effect of soil moisture and thaw depth on methane flux from wet coastal tundra ecosystems on the north slope of Alaska. *Chemosphere*, **26**, 329–338.
- Watanabe, K., Ezaki, T., Fukumura, K., Mizoguchi, M. and Kiyosawa, H. (2001): Variability of thaw depth depending on surface micro-undulation and vegetation cover in the Siberian Tundra. *Proceedings of the Fifth International Study Conference on GEWEX in Asia and GAME*. GAME Publ., **31**, 632–636.
- Watanabe, K. and Mizoguchi, M. (1998): Pit observations of layer in tundra wetland near Tiksi, Siberia.

- Activity Report of GAME-Siberia. GAME Publ., **14**, 37–42.
- Watanabe, K., Mizoguchi, M., Kiyosawa, H. and Kodama, Y. (2000): Properties and horizons of active layer soils in tundra at Tiksi, Siberia. J. Jap. Soc. Hydrol. Water Resour., **13**, 9–16.
- Whittaker, R.H. (1975): Communities and Ecosystems. New York., MacMillan, 438 p.
- Zamolodchikov, D.G., Karelin, D.V. and Ivashchenko, A.I. (1997): Carbon balance of tundra landscape in central Siberia: observations, simulation and GIS. J. Gen. Biol., **58**, 15–34.
- Zimov, S.A., Zimova, G.M., Daviodov, S.P., Daviodova, A.I., Voropaev, Y.V., Voropaeva, Z.V., Prosiannikov, S.F. and Prosiannikova, O.V. (1993): Winter biotic activity and production of CO₂ in Siberian soils: A factor in the greenhouse effect. J. Geophys. Res., **98 (D3)**, 5017–5023.
- Zimov, S.A., Davidov, S.P., Voropaev, Y.V., Prosiannikov, S.F., Semiletov, I.P., Chapin, M.C. and Chapin, F.S. III (1996): Siberian CO₂ efflux in winter as a CO₂ source and cause of seasonality in atmospheric CO₂. Climatic Change, **33**, 111–120.

(Received March 29, 2002; Revised manuscript accepted October 15, 2002)