Dynamics of CO$_2$ evolution of Arctic soils from Northern Siberia and Scandinavia

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1. INTRODUCTION

Growing interest in soil respiration in Arctic environments has opened wide research fields in microbial physiology and models associated therewith (Shivaji 2004). Much interest has been focused on metabolism in cold environments, with special emphasis on CO$_2$ and CH$_4$ evolution from tundra soils (Nadelhoffer et al. 1997, Vourlitis and Oechel 1997a,b). For modeling approaches, however, it is important to include the variability of microbial communities and their reactions to temperature shifts, i.e., the possible individual adaptations to temperature spans and related shifts in Q$_{10}$ values of metabolic activity, which may indicate significant alterations in metabolic processes that point to important ecological factors to consider in the study of soil biological processes (Nadelhoffer et al. 1991, Sjögertsen and Wookey 2002). Special attention must be paid to processes at the cellular and subcellular level, and to the enzymes and substrates involved: an investigative effort that constitutes a crucial step in linking landscape modeling to small-scale processes.

Soil carbon loss, generally termed soil respiration, is principally due to microbial and root respiration. Its measure can be defined in three ways (Haber 1958), i) the "physiological line", ii) the "physical line", and iii) the "ecological line". The physiological line is mainly focused on the efficiency of soil organisms (and roots) and the reaction potential to the various environmental influences. The physical line emphasizes the interactions between the soil and atmosphere, including processes of diffusion and physico-chemical CO$_2$ balances. The last one, the ecological line, stresses soil respiration in an ecosystematic context. Both the physiological and the ecological lines are related to the main environmental factors, namely, temperature, moisture, and available nutrients. These factors can be summarized as stressors, which act at the environmental, cellular and subcellular levels (Bölter et al. 2003a, Bölter 2004).

The ecological level, i.e., the understanding of soil respiration at the level of the ecosystem, has been the main focus in tundra environments for the past several years. Different attempts at modeling have been a part of this picture (e.g., Shaver 1996, Rastetter et al. 1997, Moorhead and Reynolds 1996, Ostendorf et al. 1996). Evolution of CO$_2$ in these environments has become of special importance when connected to related C storages, as recently summarized by Lal et al. (2000) and Kimble (2004).

The step from physiology to ecology, however, is only poorly emphasized in ecological studies, like the step from the micro site to the landscape (Sommerkorn 1998). The use of models for soil respiration further have mostly ignored the special patterns of physiological items, although its temperature sensitivity, as expressed by the Q$_{10}$, is widely known and used as an indicator to describe affects of temperature on soil monitored respiration patterns (Coyne and Kelley 1978, Lloyd and Tailor 1994, Panikov 1997) or growth rates (Gounot and Russell 1999).

This paper compares respiration data from different Arctic environments by using the Q$_{10}$ values of respiratory activity. The locations cover a Siberian tundra site (Lena Delta), a Finnish fjell (Jauristunturit) and agricultural Norwegian sites (Alta). Although these studies were

performed for different purposes, the results of the local respiratory activity provide insights into local physiological properties and potentials of respiration.

2. MATERIALS AND METHODS

2.1 Study sites

The locations of the studies in Siberia and Scandinavia are displayed in Fig. 1.

a) Russia (Siberia), Samoylov Island, Lena Delta. The island is located in the central part of the Lena Delta (72° N, 126° E). The soils are derived from Holocene sediments. According to the US Soil Taxonomy (1998) the soils of the investigation sites can be differentiated into Typic Psammoturbels, Ruptic Historels and Glacic Aquiturbels (Müller-Lupp 2002). The temperature conditions for the nearest weather station (Tiksi) show mean daily minima between -36 and +4 °C, mean daily maxima between -29 and +11 °C. Yearly precipitation is 200-250 mm (period: 1961-1990; www.worldweather.org). More detailed descriptions of samplings and the soil profiles can be found in Rachold (1999 and 2000).

b) Finland (and Norway), Jauristunturit . The fjell (=mountain region) is located in the border region of Norway and Finland at about 550 m a.s.l. (68° 50' N, 23° 50' E). The mean annual temperature of the nearest weather station Siccajarvi is -3.1 °C, and mean precipitation is 366 mm (DNMI 1999). At this site Podzols have developed on coarse morainic ground covered by lichen heath and various shrubs. Further, Regosols and Cambisols have been described during a recent study (Uhlig and Zink 2005).

Finland, Vuotso. This area is located in a forested area near the village Vuotso in Lapland (68° 10'N, 26° 45' E). The soils have been developed from different parent materials (glacial till and glaciofluvial sand) and comprise mostly podzols (Peth and Horn 2005). The vegetation is dominated by spruce, birch and several shrubs. The mean temperature of the nearest weather station (Sodankylä 67° 22' N, 26° 39' E) in summer is 20 °C and in winter is -18 °C.

c) Norway, Alta. The two sampling sites in this area (Flaten and Tverrelvdalen) are located near Alta (70° N, 23° 20' E). The yearly average minimum temperature is -9°C, the average maximum is +16 °C (www.tutiempo.net). The soils are Stagnic Luvisols, Stagnic Cambisols (Pseudogley: AG Boden 1994).
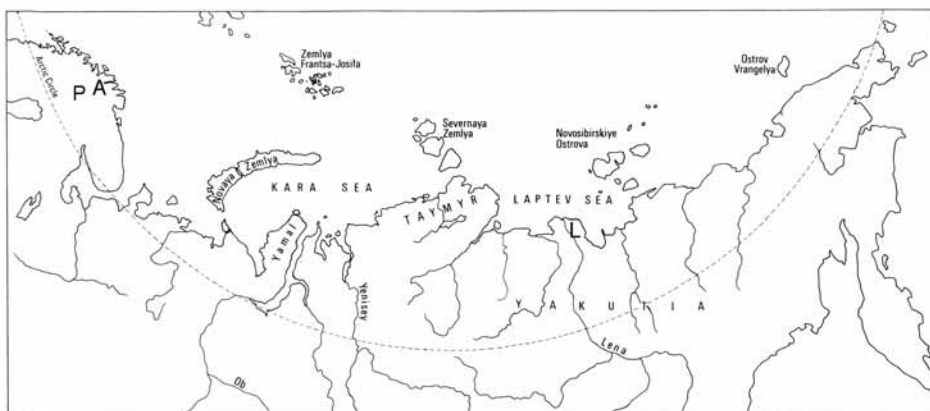

Fig. 1. Sampling locations in Siberia (L, Lena Delta) and Scandinavia (P: Pöyrisjärvi, Finland, A: Alta, Norway).

2.2 Respiration measurements.

a) Samoylov Island. Field measurements were carried out with a CO$_2$-analyser unit (Rosemount, Germany), temperature controlled mini-cuvette chamber, gas flow pumps and a programming and data storage unit. Field data were obtained during summer 1998 and 1999 (Sommerkorn 1999, Müller-Lupp 2002, Bölter et al. 2003b). Samples were taken from surface layers down to the permafrost in varying steps, depending on the actual soil horizons.

b) Jauristuntirit and Vuotso. Samples were transported dry and cool to the laboratory in Kiel and analysed using a temperature controlled CO$_2$-analyser device (Walz Co., Effeltrich, Germany). Temperature steps were 5 °C for incubations from +5 to +40 °C (Bölter 1994). Samples were taken from surface horizons (0-4 cm) during summer 2002. The sites in the Jauristunturit region were take with respect to grazing as follows: Norway (non-grazed winter pasture), Finland (strongly grazed year-around pasture), and an intermediate stage grazing since 1990. The Vuotso sites were sampled at forest floors in different areas.

c) Alta. Basal respiration and substrate-induced respiration (SIR) measurements were carried out shortly after sampling in a lab in Tromsö according to the titration method of Isermeyer (1952, modified after Öhlinger 1993). Incubation time was set for 3 days, incubation temperatures were ambient local temperature and 21 °C; the Q$_{10}$ values were calculated with respect to the individual temperature spans. Samples were taken from different depth layers according to soil horizons during spring 1999. Temperature measurements were performed by temperature sensors and loggers as well as by hand; they are partly interpolated. The sites were M1 and M2 on a meadow, a wheel track (Track) on this meadow, and sites in birch (BF) and spruce (SF) forests.

2.3 Calculation of Q$_{10}$

Q$_{10}$ values for individual °C intervals were calculated from the approximated temperature model (Hochachka and Somero 1984):

Q$_{10}$ = (R1/R2) ^ 10/(T2-T1)

where

Q$_{10}$:   temperature coefficient
R1, R2:   respiration rates at T1, T2
T1, T2:   measured temperatures

3. RESULTS

3.1 Russia (Siberia) Samoylov Island, Lena Delta.

The soil respiration data of the tundra environment at Samoylov Island show great variability with soil depth. Clear relationships are evident to temperature, respiration rates increasing at all depths with increasing temperature. But correlations with total soil organic matter could not be found, as shown by example for Plot 3 (Fig. 2 and 3). There are also no direct relationships between corresponding Q$_{10}$ values and soil organic matter or soil depths. Similar figures can be found for respiration data from other plots analysed for CO$_2$ evolution in this field.

The related Q$_{10}$ values for these respiration activities are given in Table 1. Despite the different ranges, all values are recalculated to comport with the 10-centigrade temperature span. The individual data show great variability. Very high figures (>5) can be found several times. High Q$_{10}$ values are mostly found at low starting points, i.e., temperature spans that include low temperatures. There was no relationship found to soil depth, which could have been assumed in relation to distributions of soil organic matter or biomass, or of numbers of soil organisms(the last three items not shown here).
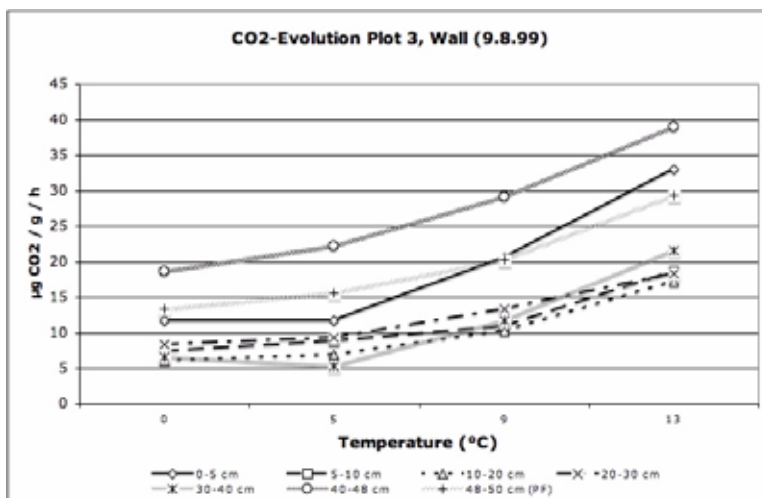
Fig. 2. CO_2 evolution from soil samples taken from different depth layers at Plot 3 (edge of a polygon, analyzed August 9, 1999) at Samoylov Island (Lena Delta, Siberia).
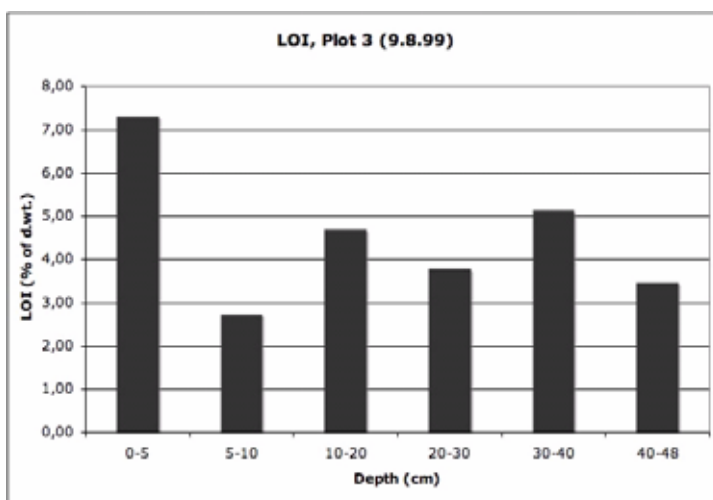

Fig. 3. Soil organic matter contents (LOI) from Plot 3, Samoylov Island, Lena Delta.

3.2 Finland, Vuotso and Jauristunturit.

The data from Finland (Jauristuntirit and Vuotso) do not show any correlation between total organic matter (loss on ignition) and the related Q_{10} values (Fig. 4a-c). A summary of the data with respect to the sites is presented in Table 2. These data show a much more homogeneous situation than those from Siberia. There is much less variability of the Q_{10} values, cf. minimal and maximal data of the different data sets, especially with respect to extreme high values. Highest mean values can be found for the temperature ranges from 10-20 and 15-25 centigrade. The ranges above and below show smaller values, but a clear tendency toward decreasing Q_{10} values with increasing temperature spans cannot be validated (Fig. 4a-c). Further, clear separations between the sites with respect to mean values and spans (min-max) are not evident from these data.

Table 1. Q$_{10}$ values of soil samples from profiles at Samoylov Island, Lena Delta, Siberia.

Plot	Location.	Depth (cm)	T.span (°C)					
			0-5	5-9	9-13	0-9	0-13	5-13
2	center	0-5	9.02	7.08	4.01	8.10	6.52	5.33
		5-10	12.76	7.19	2.64	9.89	6.59	4.36
		10-20		8.96		15.78		
		20-30	3.44	6.80	3.27	4.66	4.18	4.72
		30-40	5.30		3.57	16.46	10.28	15.56
		40-50		5.66	6.46	11.51	9.64	6.05
		50-60	1.49	3.89	2.78	2.28	2.42	3.28
		60-70	1.42	2.64		1.87		
2	near crack	0-5	1.83	5.36	3.13	2.95	3.00	4.09
		5-12	14.46	6.42	2.99	10.08	6.94	4.38
		12-19	4.00	4.54	13.91	4.23	6.10	7.95
		19-25	3.10		5.09	7.35	6.56	10.49
		25-31	1.40	7.42	3.71	2.94	3.15	5.25
		35-43	9.00	4.23	6.59	6.43	6.48	5.28
		43-49	5.55		4.59	10.63	8.21	10.49
		49-57	1.19	5.63	6.92	2.38	3.30	6.24
		57-70	1.00		3.01	7.34	5.58	16.34
		70-72	1.21	7.41	3.60	2.71	2.96	5.17
3	wall	0-5	1.00	4.16	3.21	1.89	2.22	3.66
		5-10	1.42	1.71	3.86	1.54	2.04	2.57
		10-20	1.31	2.76	3.57	1.82	2.24	3.14
		20-30	1.25	2.45	2.21	1.69	1.83	2.33
		30-40	0.65	6.94	4.63	1.87	2.47	5.67
		40-48	1.42	1.96	2.06	1.64	1.76	2.01
		48-50	1.38	1.93	2.50	1.60	1.84	2.19
3	center, moos cover	0-5	1.60	4.94	4.21	2.65	3.05	4.56
		5-15	3.45	11.06	1.80	5.79	4.04	4.46
		10-20	1.40	8.78	5.66	3.16	3.78	7.05
		15-20	0.53	15.59	7.59	2.38	3.40	10.88
		20-25	1.21	3.75	1.94	2.00	1.98	2.70
3	near crack	0-4	1.52	7.59	3.74	3.10	3.28	5.33
		4-8	1.66	3.88		2.42		
		35-39	1.78	9.91	4.35	3.81	3.97	6.56
3	profile I	0-8		2.25	2.61			2.42
		8-11		4.21	4.82			4.50
		11-16	1.65	5.63	4.58	2.85	3.30	5.08
		16-18	3.23	17.20	3.44	6.79	5.51	7.69
		18-24	2.24		7.90	8.68	8.43	19.32
		24-28		1.33	2.36			1.77
		28-32		4.96	4.29			4.62
		32- pf	5.76	8.34	3.84	6.79	5.70	5.66
3	profile II	20-26	2.79		11.11	8.72	9.40	20.09
		26-37	1.56	18.33		4.66	8.43	
		37-48	1.90	3.91		2.62	5.13	9.56

3.3 Norway, Alta.

Table 3 summarizes the data obtained at the sites in Norway. These data are comparable to those from Finland. They do not show great variability, neither with respect to sites or depths, nor to seasonal aspects. The total range for the Q_{10} values is even lower than for the Finnish sites and can be found between 0.62 and 3.8, although the actual temperature span is between 0 and 23 °C. Longer incubation time for respiration from 3 to 5 days (data not shown here) also do not show significant changes for the individual Q_{10} values.

4. DISCUSSION

The most significant climatic and nutritional conditions in polar regions pose various stress factors to soil organisms. These are frequent freeze-thaw cycles, dry-wet situations, and strong competition for both nutrients and favorable habitats. This situation presents a need for a wide range not of adaptations to specific conditions, but of life processes. Vegetation patterns and plant growth forms change drastically within distances of few meters due to small-scale patterns of topography and related variables of hydrology and soil chemistry, as expressed by soil and vegetation patterns (Bliss 1981; Bliss et al 1984; Gebauer et al. 1995; Chapin et al. 1988, Beyer et al. 2002, Blume et al. 2002). Moisture and micro-environmental habitats are the dominant factors that set the frames for tundra ecosystems (Wynn-Williams 1990; Kennedy 1993). Wet tundra systems need metabolic mechanisms for shifting water levels, i.e., varying oxygen saturation conditions, while fjells and northern forest ecosystems have generally a low nutrient status, low production
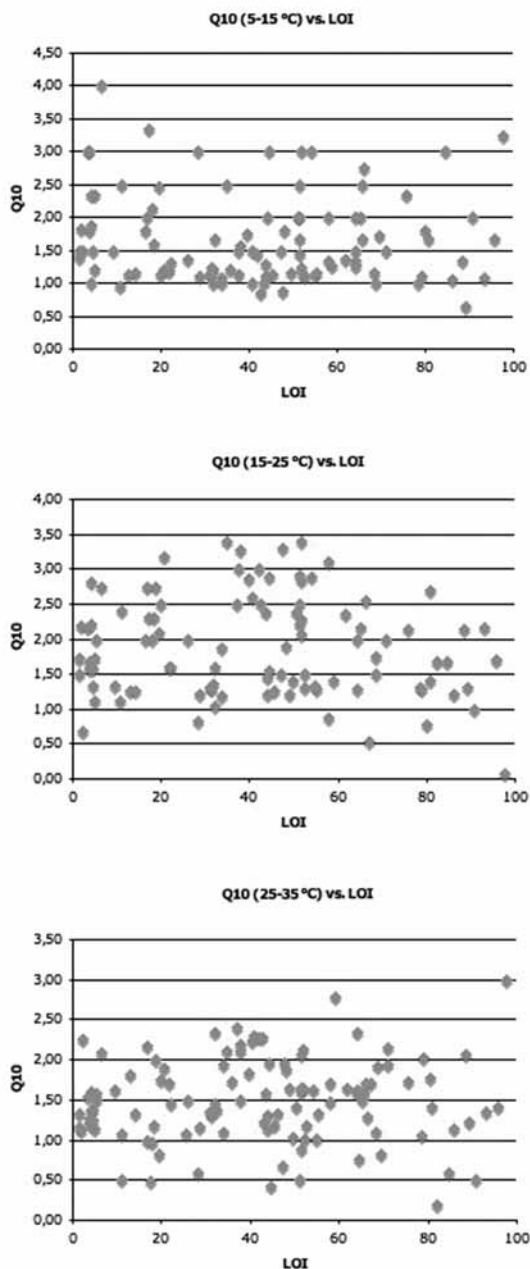

Fig. 4. Relationships between loss on ignition (LOI) and Q_{10} values for different temperature steps. A) 5-15 °C (upper graph), B) 15-25 °C (middle graph), and C) 25-35 °C (lower graph).

rates and low decomposition activity (Heal 1981; Bliss et al. 1984; Binkley and Högberg 1997; Bhatti et al. 2002). Further, the latter regions are under varied agricultural usage, from cropping to different types of grazing (Forbes et al. 2005).

The data presented for the different types of arctic soils indicate that their behavior differs, as indicated by Q_{10} values, with regard to the effect of temperature on respiration. While the tundra soils from Siberia have wide ranges in Q_{10} value (Table 1), the soils from northern Scandinavia display only lower ranges (Table 2 and 3). This can be attributed to factors related to environmental constraint as well as to differences in microbial communities. The microbial community under such influence can be regarded as highly diverse and rich (Fierer et al. 2002), and thus can react appropriately to these most rigorous environmental changes. This sort of response can be judged by noting the different temperature optima, which have been found for dry tundra soils in Finland at between 15 and 25 °C (Bölter and Möller 2005), and in boreal coniferous forests at between 7 and 12 °C (Huxman et al. 2003). Further, Lipson et al. (2002) showed different reactions in soil respiration between temperatures in winter and summer. Such physiological mechanisms point not only to temperature control of individual processes, but also to specific controls on wider metabolic process chains, influenced by gene expressions

Table 2. Summarized data for soil respiration Q_{10} values from samples taken in Finland at Vuotso (forest sites) and Jauristunturit (fjell sites in Norway, Finland) for different temperature spans. Presented are number of data (N), mean values (mean) as well as minima (min) and maxima (max) of the individual data sets.

		T-span (°C)				
		5-15	10-20	15-25	20-30	25-35
All data	N	101	98	100	112	113
	mean	1.66	2.09	1.89	1.57	1.5
	min	0.64	0.5	0.08	0.05	0.2
	max	4	4.5	3.4	2.75	3
Vuotso	N	28	28	31	30	31
	mean	2.15	2.48	1.73	1.14	1.24
	min	1	1	0.08	0.05	0.2
	max	4	4.5	2.82	1.79	3
Jauristunturit						
Norway	N	36	35	38	41	40
	mean	1.42	1.89	1.96	1.72	1.64
	min	0.64	1.15	0.78	0.48	1.02
	max	3	3.43	3.29	2.6	2.79
Finland	N	16	16	10	18	19
	mean	1.55	1.94	1.96	1.91	1.52
	min	0.96	0.5	1.04	0.84	0.5
	max	2.5	3.25	3.4	2.6	2.33
Transition	N	18	16	18	20	20
	mean	1.53	2.09	2.02	1.57	1.57
	min	0.86	1.12	0.53	0.62	0.48
	max	3.33	3.33	3.4	2.56	2.27

Table 3. Soil temperature (T) amd Q10 values for soil respiration from different sites in Northern Norway during spring season 1999; M1, M2: meadow; BF: birch forest; SF: spruce forest. Data are not available for all samplings.

Location	Depth (cm)	13.5. Q_{10}	13.5. T	19.5. Q_{10}	19.5. T	25.5. Q_{10}	25.5. T	31.5. Q_{10}	31.5. T	6.6. Q_{10}	6.6. T	12.6. Q_{10}	12.6. T	18.6. Q_{10}	18.6. T	24.6. Q_{10}	24.6. T	30.6. Q_{10}	30.6. T
M1	0-5			2.19	9.0	2.07	9.0	2.61	6.0	2.39	11.0	2.11	12.0	2.23	11.0	2.37	8.0		
	5-10			2.19		2.36		2.36		2.89	9.0	2.17	11.0	2.36	10.5	2.44	7.5		
	20-25			2.48	0.0	2.20		2.14		2.25	6.0	2.23	7.5	2.12	8.0	2.07	6.0		
Track	0-5	2.55	6.0	2.03	9.0	1.97	9.0	2.07	9.0	2.04	8.0	1.32	11.0	1.89	12.0	1.83	8.0	2.26	12.0
	5-10	2.77		2.15		2.52		2.08		2.00	7.5	2.35	10.5	2.44	10.0	2.08	7.5	2.31	12.0
	20-25		0.0		0.0	1.73		2.50		2.17	7.0	2.32	8.0	2.10	7.0	2.11	6.0	1.63	9.0
M2	0-5			2.93	6.0	2.06	9.0	2.18	9.0	2.37	8.0	2.36	13.0	2.37	12.5	2.36	11.0		23.0
	5-10			2.33		2.49		2.44		2.42	7.0	2.31	12.0	2.48	12.0	2.40	10.5	2.79	22.0
	20-25			2.4		2.32		1.99		2.87	7.0	2.30	9.5	2.40	11.0	2.37	10.0	2.03	17.0
BF	litter			1.85	5.0	2.00	3.0	2.00	4.0	1.77	4.0	1.62	12.0	2.33	7.0	2.51	6.5	1.55	14.0
	0-5					2.43		2.51		2.33	3.0	2.19	7.0	2.35	7.0	2.18	6.5	2.12	12.5
	5-10					2.42		2.35		2.93	3.0	2.90	6.0	2.43	6.5	2.17	6.5	2.23	12.0
	15-20							3.61				2.68	6.0	2.57	6.5	1.96	6.0	1.52	10.0
SF	litter							2.34	2.0	2.54	3.5	2.24	6.0	1.81	7.0	1.96	7.0	1.16	13.0
	0-5							2.71		2.80	3.0	2.50	3.0	2.17	6.0	2.09	6.0		10.0
	5-10							3.48		3.80	3.5	3.61	3.0		5.0	1.94	6.0	1.61	10.0
	15-20										2.0	3.54	2.0		5.0			1.80	9.0

for specific environmental conditions, or by community changes due to changes in the physico-chemical environment. Extreme high values (>50) have been monitored at some places (not shown here), but they could not be seen in relation to actual metabolic processes. Mikan et al. (2002) interpret their high Q_{10} values (63 – 237) as signs of extra cellular and intracellular physical effects.

Q_{10} values thus can be regarded as indicators not only for individual reactions but also for enzymatic nets and gene expressions. Although Q_{10} values are found in ranges of 2 to 5 (Coyne and Kelley 1978, Raich and Schlesinger 1992, Kätterer et al. 1998), shifts in Q_{10} values with respect to temperature have been found in several studies and considered to be related to activation energy of special processes (Schleser 1982, Lloyd and Taylor 1994, Widen 2001, Sjögertsen and Wookey 2002). Highest shifts in Q_{10} values were monitored at low temperatures, specifically in ranges between 0 and 10 °C (Nadelhoffer et al. 1991, Sjögertsen and Wookey 2002, Mikan et al. 2002), and for Antarctic soils maximal Q_{10} values for soil respiration were found for temperatures between 5 and 15 °C (Bölter 1990, Bölter et al. 2002, Roser et al. 1993). On the other hand, Kerry (1990) reports, regarding fungi isolated from soils in Wilkes Land, that many of them showed *lowest* Q_{10} values for the temperature range between 4 and 15 °C. Smith (2003) refers to an indication of a mixed community with different responses to temperature. For some studies, direct impacts on the soil environment by grazing were also regarded as a factor for shifting Q_{10} values (Cao et al. 2004). Elevated Q_{10} values at low temperatures seem contradictory to the generally accepted belief that higher temperatures create a higher metabolic activity. Reviewing large number of soil respiration data, Kätterer al. (1998) presented Q_{10} values for soil respiration at around 2. Decreasing Q_{10} values with increasing incubation temperatures were found by Dalias et al. (2001) in coniferous forests during straw mineralisation as well as in other environments (Lloyd and Taylor 1994, Kirschbaum 1995), whereas Nadelhoffer et al. (1991) and Howard and Howard (1993) reported increasing Q_{10} values with increasing temperature.

Organisms in polar environments often have to cope with the situation in which increased temperatures lead to drought stress. Osmotrophic organisms like bacteria and fungi find themselves in a pair of shears represented by precarious water availability on one hand and low nutrient conditions on the other. Hence, not only water stress hampers potential microbial activity, but also increasing concentrations of free anions and cations in the remaining fluid water increase an osmotic stress factor, which calls for a concomitant high tolerance of the organisms to this hardship (Bölter et al. 2003a, Bölter 2004). The overall metabolic changes indicate that such a hazardous environment has imposed (and which may drastically change minute by minute) seems to be more important to livelihood than the adaptation to a single variable such as low temperature. It now appears important to determine the special constraints and thresholds that have to be regarded as active switches for metabolic processes. The microclimatic conditions with drastic changes at the 0 °C threshold can be counted as one of these important switches (Walton 1982; Morley et al. 1983), the observations of Mikan et al. (2003) that Q_{10} values shift strongly when T < 0 °C being of major significance in this regard.

The strong differences in our data indicate that further stimulating factors must also be present, but that temperature triggers them, leading to the clear inference that temperature in Siberian tundra systems is a stronger limiting item than in the Scandinavian soils. Hence, other factors such as nutrient availability are relegated to a role of lesser importance. Another explanation may be that maintenance respiration is more sensitive to changes in temperature than to other factors, as described for plant respiration by Ryan (1991). When adapting this to the microbial metabolic processes, we can suspect that these organisms are under permanent limiting conditions and that temperature, i.e., the total energy input into the system, is the most crucial factor for its reactivity. Thus, the question arises whether temperature is a real driving force in this system or whether it acts just as a limiting unit. Dalias et al (2001) found that

decreasing Q_{10} values along with increasing temperatures were affected by available organic matter and harmful microbial products (wastes), which were formed at higher temperatures. Hence, conflicting processes between the physico-chemical enzyme reactions and the biological processes of decomposition are reflected in this quotient, which thus not only reflects temperature responses but also mirrors a more complex system of ecological effects. All these have to be considered carefully when modeling large tundra ecosystems, especially in those seasons with temperatures just above the zero curtain.

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