

Short term changes of microbial processes in Icelandic soils to increasing temperatures

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Received: 26 May 2009 – Published in Biogeosciences Discuss.: 9 July 2009

Revised: 15 December 2009 – Accepted: 29 January 2010 – Published: 17 February 2010

Abstract. Temperature change is acknowledged to have a significant effect on soil biological processes and the corresponding sequestration of carbon and cycling of nutrients. Soils at high latitudes are likely to be particularly impacted by increases in temperature. Icelandic soils experience unusually frequent freeze and thaw cycles compare to other Arctic regions, which are increasing due to a warming climate. As a consequence these soils are frequently affected by short term temperature fluctuations.

In this study, the short term response of a range of soil microbial parameters (respiration, nutrient availability, microbial biomass carbon, arylphosphatase and dehydrogenase activity) to temperature changes was measured in sub-arctic soils collected from across Iceland. Sample sites reflected two soil temperature regimes (cryic and frigid) and two land uses (pasture and arable). The soils were sampled from the field frozen, equilibrated at -20°C and then incubated for two weeks at -10°C , -2°C , $+2^{\circ}\text{C}$ and $+10^{\circ}\text{C}$. Respiration and enzymatic activity were temperature dependent. The soil temperature regime affected the soil microbial biomass carbon sensitivity to temperatures. When soils were sampled from the cryic temperature regime a decreasing soil microbial biomass was detected when temperatures rose above the freezing point. Frigid soils, sampled from milder climatic conditions, were unaffected by difference in temperatures. Nitrogen mineralisation did not change with temperature. At -10°C , dissolved organic carbon accounted for 88% of the fraction of labile carbon which was significantly greater than that recorded at $+10^{\circ}\text{C}$ when dissolved organic carbon accounted for as low as 42% of the labile carbon fraction.

1 Introduction

The Arctic contains about 11% of global soil organic matter (SOM) (Schimel and Mikan, 2005) while those areas referred to as “high-latitude ecosystems” may contain as much as 60% of global SOM (Hobbie et al., 2000). High latitude regions are experiencing the most significant impacts of climate changes (Serreze et al., 2000; Schimel and Mikan, 2005) and this could result in the release of SOM in the future. It is acknowledged that the soil microbial biomass is active during sub-zero temperatures in winter months (e.g., Clein and Schimel, 1995; Mikan et al., 2002; Schimel and Mikan, 2005) because soil particles maintain liquid water films at temperatures down to -10°C (Price and Sowers, 2004). Until now, most research has focussed on the high arctic environments (e.g., Mikan et al., 2002; Schimel and Mikan, 2005; Edwards et al., 2006) and the taiga (e.g., Schimel and Clein, 1996; Rodionow et al., 2006) where soils, impacted by permafrost, have limited pedological development. There has been little consideration of more mature soils or those at the margins of agricultural latitudes.

Controlled laboratory studies have frequently been used for studying the effect of temperature on soil biological parameters (e.g., Clein and Schimel, 1995; Schimel and Mikan, 2005; Panikov et al., 2006) as they enable experimental control with homogenised samples, thus removing some of the uncertainty associated with field conditions. Moreover, field measurements may not reflect the actual dependence of microbial respiration, as in the field, soil respiration is the product of both root and microbial respiration, which in turn have different temperature responses (Boone et al., 1998). Long-term incubation experiments have been criticized as they may not reflect the actual temperature dependence of microbial respiration and may underestimate the temperature



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sensitivity of rapidly depleted labile substrate pools (Boone et al., 1998; Reichstein et al., 2000). Furthermore mineral transformations in long term experiments may exaggerate measured microbial responses and experimental sensitivity may be compromised (Mikan et al., 2002). Short term incubations have been recommended for overcoming such effects (Boone et al., 1998; Reichstein et al., 2000; Mikan et al., 2002). Studying short term temperature changes are likewise believed to be worthy of consideration as they can give early indication of the impact of climate change on soil C dynamics (Boddy et al., 2008; Belay-Tedla et al., 2009).

Iceland lies between 63 and 67° N and has a landmass of 103 000 km². The climate is sub-arctic in the lowlands but arctic at higher elevations and the resultant soils are described as forming in cryic and frigid zones (Arnalds and Kimble, 2001). In Iceland, permafrost, is not wide spread, being found in isolated areas in the interior (Thorhallsdottir, 1997). All soils, however, are exposed to annual freezing cycles between November and May. Iceland has the most extensive area of Andosols (volcanic soils) in Europe (Arnalds, 2004) and these soils have a propensity for high organic carbon and nitrogen sequestration (Palmason et al., 1996; Gudmundsson et al., 2004). Icelandic soils are estimated to store up to 2.1×10^9 t of soil organic carbon (Oskarsson et al., 2004). Despite the relative harshness of the Icelandic climate, these soils are highly fertile although the need for land drainage makes effective soil management a considerable undertaking. The soils of Iceland experience unusually frequent freeze and thaw cycles, more than any other sub-arctic region (Orradottir 2002; Orradottir et al., 2008). Freeze and thaw cycles make decomposition processes in cold regions complex due to persistent microbial activity at low temperatures, interaction of the quality and supply of substrates as well as microclimate limitation to soil respiration (Barret et al., 2006). Temperature changes in the short term during freeze and thaw periods are likely to affect the cycling of carbon by microorganisms in Icelandic soils.

While there is a broad understanding of the physical and chemical attributes of Icelandic soils (Arnalds, 2004), there have been few biological investigations. Most soil studies have focussed on agronomical aspects and Gudmundsson et al. (2004) highlighted the inherent N limitation in these soils. Gudmundsson et al. (2004) and Ritter (2007) have postulated that these soils are associated with very significant N immobilization, but these observations have not been accompanied with empirical biological evidence.

Many techniques are available to study microbial community, size, activity and function in soils. In the case of this study a brief justification of selected methods can be made. The soil microbial biomass utilises the labile fraction of soil organic matter, transforming and cycling organic matter within the soil. Enzyme activities reflect the metabolic activity of key soil processes thus reflecting the responsiveness of the soil microbial biomass (mic_c) (Gianfreda et al., 2005). Soil respiration (C_{min}) is a measure of heterotrophic

activity of the microbial biomass (Dawson et al., 2007). KCl extractable NH_4^+ and NO_3^- has been interpreted as a measure of soil exchangeable N (Bremner, 1965) and has frequently been used for estimating the net N mineralization, nitrification and ammonification rates (Raison et al., 1987). While various assays have been developed for the measurement of net N_{min} (Curtin and McCallum, 2004), workers have considered that the difference in initial versus final concentration of mineral N (NO_3^- and NH_4^+) can offer an adequate estimation of total N_{min} (Raison et al., 1987; Miller et al., 2007).

Such diverse measurements of soil microbial parameters require a degree of integration to place the measured values in a context. The widely adopted Q_{10} value is the factor by which a 10 °C increase in temperature will increase the measured physiological response. The respiration coefficient Q_{10} is commonly used as an index of temperature dependence (Mikan et al., 2002). The metabolic quotient ($q\text{CO}_2$) of the soil micro-flora (Odum, 1969) describes the ratio of respired C to assimilated biomass C and provides a comparative evaluation of the physiological condition of the soil microbial community. The soil $q\text{CO}_2$ has been used as an indicator of stress as soil microorganisms divert more energy from growth into maintenance as stress increases (Killham, 1985). Anderson and Domsch (1993) used the $q\text{CO}_2$ while making an assessment of the effect of temperature on soil.

The primary aim of this study was to assess the short term response of soil microbial processes and nutrients dynamics in Icelandic soils to changes in temperatures. The effect of different land use and soil temperature regimes was further studied by sampling soils from three treatment plots, grass, barley and controls located in both cryic and frigid soil temperature regimes. Soil microbial processes were studied by subjecting soils to temperatures both below and above the freezing point and measuring the total microbial biomass carbon, dissolved organic carbon, respiration, enzymatic activity and N mineralisation.

2 Methods

2.1 Sample preparation and selected soil measurements

Sample sites were selected to cover two soil temperature regimes and to include both grass (G) and barley (B) cultivation. Barley fields had been ploughed annually, while grass fields were ploughed at five year intervals and reseeded with suitable sward. Sample locations were: Möðruvellir (Mö_{cryic}) and Glaumbær (Gl_{cryic}) in the North with a cryic soil temperature regime and Hvanneyri ($\text{Hv}_{\text{frigid}}$) and Korpa ($\text{Kor}_{\text{frigid}}$) in the West (Fig. 1) both from a frigid temperature regime. Sampling took place at the end of April while the soils were still frozen. From each site eight replicate 8 cm diameter stainless steel cores samplers were inserted into the frozen soil (through the turf) from 0–15 cm depth and the samples were maintained frozen during their

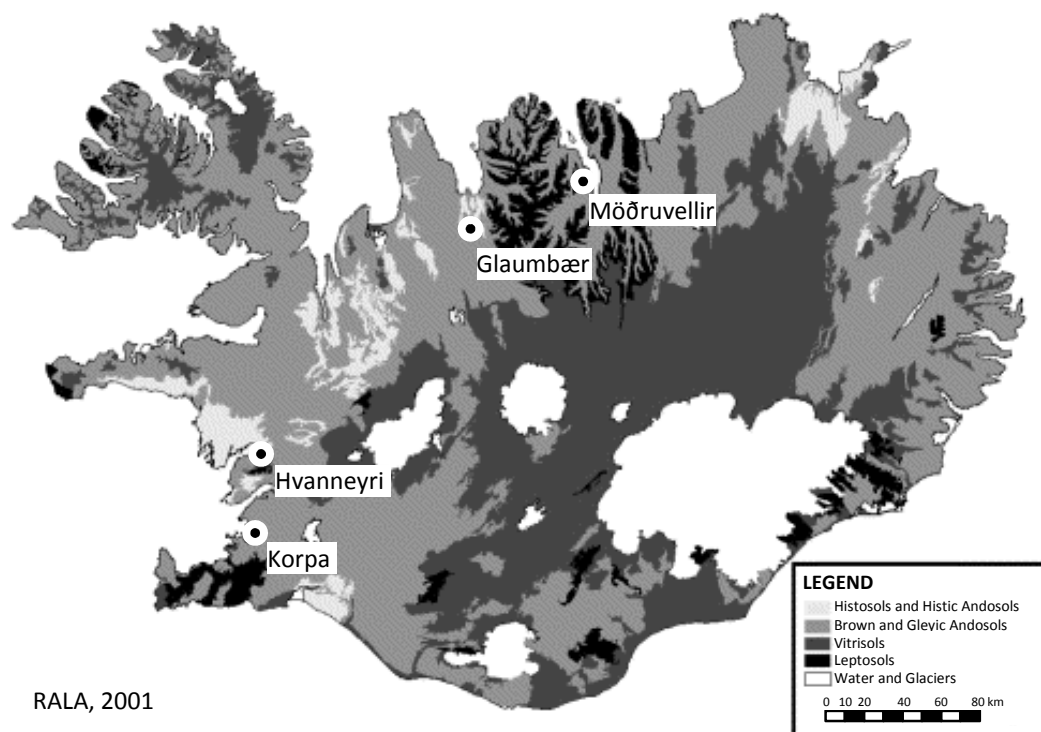


Fig. 1. A simplified soil map of Iceland with sampling locations (Modified from Arnalds and Gretarsson, 2001).

transport to Aberdeen, Scotland, where all preparatory work was conducted in a cooled laboratory. Field capacity was determined on thawed sub-samples as described by Kassel and Nielsen (1986). The eight replicate cores were hand mixed and bulked and sieved through a 3.75 mm sieve (discarding vegetative materials). All sample preparation was conducted in a cool room at +5 °C to minimise biological activity. Before all replicate subsamples were placed in incubators, soils were weighted for each measurement to be conducted in individual containers making them ready for extractions and analyses as soon as incubations ended. This allowed minimum disruption of soil microstructures after temperature treatments. Thereafter soils were frozen at −20 °C (Schimel and Mikan 2005, Clein and Schimel, 1995) for two weeks (Mikan et al., 2002). After this two week period, the soils were transferred to the four separate incubators for 2 weeks at −10 °C, −2 °C, +2 °C or +10 °C. The soils were maintained at ambient moisture content (Schimel and Mikan, 2005) which ranged from 38–59% of field capacity. These values have been reported to be optimal for soils with Andic properties (Dahlgren et al., 2004). Subsamples were taken for routine analysis (bulk density (BD), organic C, N and pH (Blakemore et al., 1987).

2.2 Microbial biomass C (mic_c)

Soil microbial biomass carbon (mic_c) was determined by chloroform fumigation (Vance et al., 1987) on all soils and

treatment temperatures after the 2 week incubation. Before incubations soils were weighted into 50 ml centrifuge bottles making them ready for extraction as soon as incubations ended. Soils were placed frozen in desiccators and were allowed to thaw during the 24 h chloroform fumigation. Non-fumigated samples were extracted immediately with 25 ml 0.5 M K_2SO_4 . Dissolved organic carbon (DOC) was analysed by an aqueous carbon analyser (LABTOC Pollution and Process Monitoring) with UV digestion and infra-red detector. The K_{EC} factor used was 0.45 (Vance et al., 1987). The 0.5 M K_2SO_4 extractable DOC from un-fumigated soils samples was used to characterize the labile carbon pool of these soils.

2.3 Soil respiration (C_{min})

Soil respiration was conducted as described by Dawson et al. (2007) by accurately weighing 1 g of field moist soil into 9 ml vacuettes before incubations. Triplicate destructive samples were maintained at −20 °C for two weeks. Thereafter samples were removed from −20 °C to 4 different incubators set at temperatures −10, −2, +2 and +10 °C. During the 2 week experiment, soil respiration was measured after 4, 8 and 14 days. Twenty four hours prior to sampling, vials were sealed and sampled using a 250 μl syringe. The CO_2 was measured using a gas chromatograph (Chrompack CP 9001) with a 2.0 m \times 1/8" \times 2.0 mm column (Porapak QS) and N_2 carrier gas (20 ml min^{-1}).

The Q_{10} value was calculated as a respiration coefficient based on cumulative CO_2 release over two weeks with a standard exponential rate equation over the defined temperature interval (van't Hoff, 1898):

$$Q_{10} = e^{(10 \cdot (\ln(R_2/R_1)/(T_2-T_1)))} \quad (1)$$

where R_1 and R_2 are respiration rates at temperatures T_1 and T_2 respectively. The $q\text{CO}_2$ value was calculated by dividing the cumulative CO_2 respired ($\mu\text{g CO}_2\text{-C g}_{\text{OC}}^{-1}$) by the microbial biomass C (expressed as $\mu\text{g-C g}_{\text{OC}}^{-1}$; Odum, 1969).

2.4 Enzymatic activity measurements

Dehydrogenase activity was measured according to a modified method by Trevors (1984) at all temperatures except at -10°C (reagents remained frozen). Prior to incubations, 1 g of field moist soil was placed into sterile darkened Universal bottles. Universal bottles with soil were placed in incubator at -20°C for two weeks. After the two week incubation at -20°C Universal bottles were placed in 4 incubators at the four experimental temperatures (-10°C , -2°C , $+2^\circ\text{C}$ and $+10^\circ\text{C}$) for two weeks. After the 2 week incubation, 10 ml 0.1 M iodinitetrazolium chloride (with 0.5 M N-tris (hydroxymethyl) methyl 1–2 aminoethane-sulfonic acid (TES), adjusted to pH 7.8 with 5 M NaOH) and placed on an end-over shaker for 18 h in incubators at, -10°C , -2°C , $+2^\circ\text{C}$ and $+10^\circ\text{C}$. At -10°C however, the added 10 ml of 0.1 M iodinitetrazolium chloride solution froze so dehydrogenase activity was not measured at that particular temperature. Thereafter 10 ml of ethanol were added and the solution centrifuged at 2750 G for 20 min. Samples were analyzed at 490 nm on a spectrometer (Cecil Instruments CE373) and quantified against a linear calibration for iodinitetrazolium formazan (INTF).

Arylphosphatase activity was measured according to Tabatabai and Bremner (1969) at all incubation temperatures except -10°C . Prior to incubations, 1 g of soil was placed in Universal bottles and incubated at -20°C for two weeks. Thereafter bottles were placed in three incubators at -2°C , $+2^\circ\text{C}$, and $+10^\circ\text{C}$ for another two weeks. After the two week incubation at -2°C , $+2^\circ\text{C}$, $+10^\circ\text{C}$, 4 ml de-ionized water, 0.25 ml toluene and 1 ml 0.015 M *p*-nitrophenyl phosphate (substrate) was added to each bottle. Thereafter bottles were sealed with glass marbles and incubated at 37°C for 1 h, after which 1 ml 0.5 M CaCl_2 and 4 ml 0.5 M NaOH was added, samples were sealed with rubber bungs and then shaken for 30 s prior to filtration (Whatman No 1). Absorbance was measured at 400 nm (Cecil Instruments CE373) and concentrations were determined against a linear calibration using *p*-nitrophenol.

The Q_{10} coefficient was calculated as activity coefficient for dehydrogenase and arylphosphatase activities for assessing both enzymes temperature dependence. Calculations Q_{10} coefficients were based on van't Hoff (1898) were R_1

and R_2 corresponded to enzyme activities at temperatures T_1 and T_2 respectively ($Q_{10} = e^{(10 \times (\ln(R_2/R_1)/(T_2-T_1)))}$).

2.5 Extractable mineral N as an estimation of N mineralization (N_{min})

Measurement of the extractable $\text{NH}_4^+\text{-N}$ and $\text{NO}_3^-\text{-N}$ were made on soils before undergoing treatments and after the two week incubation. For soils undergoing temperature treatments 5 g of field moist samples were placed in 50 ml centrifuge bottles prior to incubations at -20°C , -10°C , -2°C , $+2^\circ\text{C}$ and $+10^\circ\text{C}$. After the 2 weeks incubations soil samples were shaken in an over and under shaker for 2 h with 25 ml 2 M KCl solution, and then filtered through Whatman No 42 filter paper before quantification on a flow injection analyzer (FIAstar 5010 analyzer). All soils were extracted immediately after removal from incubators.

2.6 Data analysis

Statistical analyses were conducted using SAS 9.1 for Windows 2002–2003. After normality testing, One Way ANOVA was performed to test for significant differences between measured soil parameters, landuse systems and temperature treatments. All levels of significance are expressed as $p \leq 0.05$.

3 Results

3.1 Selected soil measurements

Soil temperature regimes and properties are summarised in Table 1. The pH values of all soils ranged from 4.3 to 6.8. BD ranged from 0.2 to 0.5 g/cm^3 , soil total C from 5.1 to 25%, soil total N from 0.5 to 1.3% and soil C:N ratio from 10.2 to 14.4. There was no general relationship between measured soil properties and soil temperature regimes (Table 1).

3.2 Microbial Biomass C (mic_c)

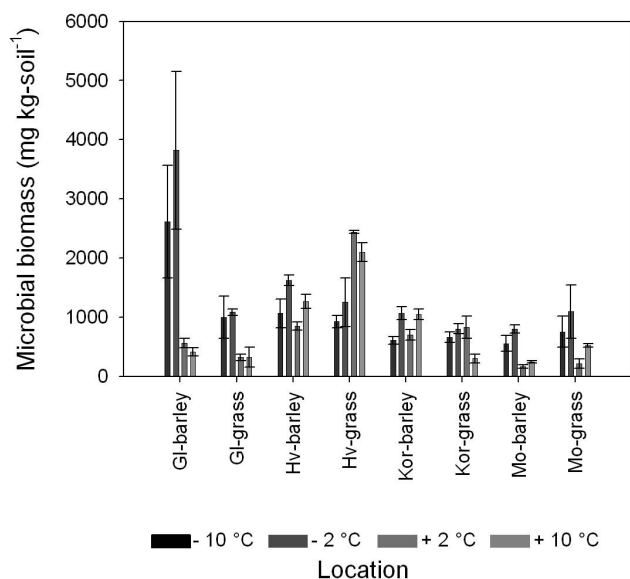
For individual soils, there was no significant difference between mic_c at each treatment temperature for soils sampled from the frigid temperature regime (Hv and Kor). Soils sampled from the cryic temperature regime (Gl and Mo) had a significantly higher mic_c at sub-zero temperatures with an abrupt decrease as temperature rose. Generally mic_c values did not differ significantly between treatment plots independent of soil temperature regime (Fig. 2).

3.3 Respiration (C_{min}) and DOC

C_{min} (cumulative CO_2 release) increased with temperatures. The highest value was at $+10^\circ\text{C}$ for all soils with the exception of Kor_{frigid}, (barley and grass) with rates higher at $+2^\circ\text{C}$ and -2°C respectively (Fig. 3). In contrast to C_{min} , DOC concentrations were generally highest at -10°C and lowest

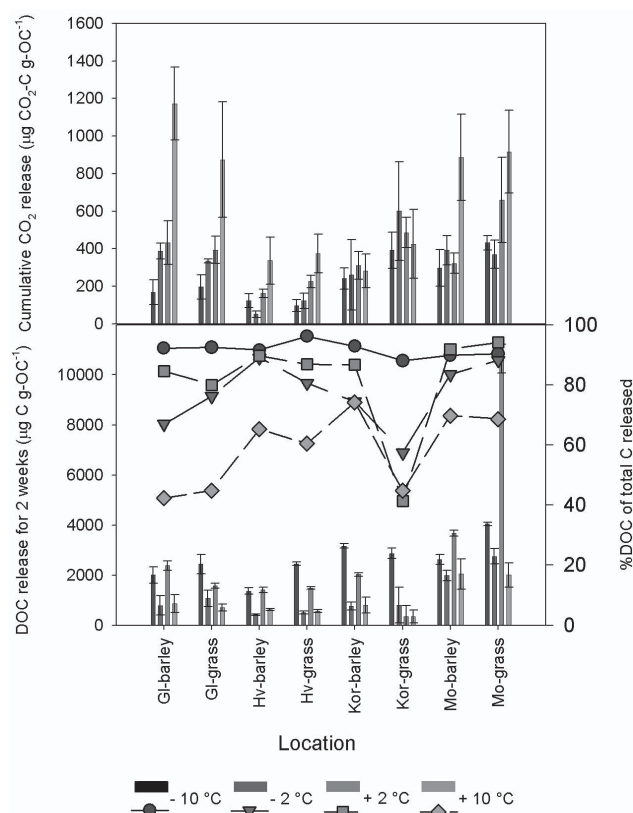
Table 1. Selected soil properties and temperature regimes for all soils, land use and temperature regime. C_{tot} denotes soil total organic carbon, N_{tot} denotes soil total organic nitrogen and BD denotes soil bulk density.

Soil temperature regime	Land use	pH H ₂ O	C_{total} %	N_{total} %	C:N	BD g cm ⁻³	Moisture %
GL _{cryic}	Barley	6.6	9.15	0.77	10.2	0.50	48.6
GL _{cryic}	Grass	6.4	9.03	0.90	11.5	0.50	50.3
Hv _{frigid}	Barley	4.5	20.0	1.30	14.4	0.30	63.0
Hv _{frigid}	Grass	4.3	25.0	1.06	13.7	0.20	60.1
Kor _{frigid}	Barley	5.4	8.65	0.77	11.2	0.50	53.5
Kor _{frigid}	Grass	5.9	9.90	0.90	11.0	0.50	53.7
Mö _{cryic}	Barley	6.4	5.95	0.44	11.8	0.50	53.6
Mö _{cryic}	Grass	7.0	5.14	0.51	11.6	0.40	65.2

**Fig. 2.** Microbial biomass for all soils, land use systems and soil temperature regime after 2 weeks incubations at -10°C , -2°C , $+2^{\circ}\text{C}$ and $+10^{\circ}\text{C}$. Columns represent mean ± 1 SE ($n = 3$). Gl=Glaumbær, Hv=Hvanneyri, Kor=Korpa, Mo=Möðruvellir.

at $+10^{\circ}\text{C}$ (Fig. 3). Moreover, DOC accounted for 88–96% of total C release (respiration + DOC) for both land uses (barley and grass) and temperature regimes (Fig. 3) at -10°C and 42–74% of total C release at $+10^{\circ}\text{C}$.

Metabolic quotients ($q\text{CO}_2$ values) for all soils (barley and grass) at all temperature treatments are shown in Fig. 4. Generally temperature did not affect the $q\text{CO}_2$ values with no significant differences being detected between temperature and $q\text{CO}_2$ values.

**Fig. 3.** Cumulative CO_2 release and DOC (from un-fumigated soil samples) after 2 weeks of incubation at -10°C , -2°C , $+2^{\circ}\text{C}$ and $+10^{\circ}\text{C}$. Columns represent mean ± 1 SE ($n = 3$) cumulative release of CO_2 and DOC of all soils, land use and soil temperature regime. The scattered symbols represent DOC percentage of total carbon released. Note the difference in scale between mineralized CO_2 and extractable DOC. Gl=Glaumbær, Hv=Hvanneyri, Kor=Korpa, Mo=Möðruvellir.

Overall, respiration Q_{10} values differed significantly between temperature intervals. There was no trend between highest and lowest Q_{10} values for temperature treatments. On most occasions the highest or lowest Q_{10} values for each soil were detected at the temperature range between -2 to $+2$ °C (Table 2). There was not a significant difference between Q_{10} values and soil temperature regime or land use (grass and barley). Calculated Q_{10} values for C_{\min} revealed that soils had lowest temperature dependencies at the coldest temperatures (-10 to -2 °C) with mean Q_{10} values of 1.14. Q_{10} values between -2 to $+2$ °C had a mean value of 4, although mean Q_{10} values were calculated to be between 1 and 2 with the exception of Hv_{frigid} barley with a value of 17.5 (Table 2). Temperature dependencies in the range of $+2$ to $+10$ °C were not significant with a mean Q_{10} values being on average 2.16.

3.4 Enzymatic measurements

For dehydrogenase activity, highest values were measured at $+10$ °C in all soils (Figs. 5 and 6). In general, the lowest activity was measured at the lowest temperature, although in four soils (Gl_{cryic} barley, Hv_{frigid} grass, Kor_{frigid} barley and Mo_{cryic} grass) activity was significantly higher at -2 °C than at $+2$ °C (Fig. 5).

Q_{10} values differed significantly between temperature intervals and were generally highest at $+2$ to $+10$ °C (Table 2). There was no trend between Q_{10} values and soil temperature regime or land use (Table 2).

Arylphosphatase activity was generally highest at $+10$ °C and lowest at -2 °C (Fig. 6). There was a significant difference in arylphosphatase activity at -2 °C compared to $+2$ °C but not in the range of $+2$ °C to $+10$ °C (Table 2). Arylphosphatase activity did not differ significantly between land use.

The arylphosphatase activity quotient Q_{10} differed significantly between temperature ranges (-2 to $+2$ °C and $+2$ to $+10$ °C). The Q_{10} was higher in the -2 °C to $+2$ °C range (except for Gl_{cryic} barley and Mo_{cryic} barley) compared to Q_{10} values in the $+2$ °C to $+10$ °C range (Table 2). This is contrary to Q_{10} values for dehydrogenase activity, which were generally higher at the $+2$ to $+10$ °C temperature range.

3.5 Extractable mineral N as an estimation of N immobilisation, nitrification and mineralization (N_{\min})

For each soil (except for Kor_{frigid} -grass), regardless of land use or soil temperature regime (cryic and frigid), net NH_4^+ -N immobilisation was the dominant process when temperatures were above zero (Fig. 7a). Where net ammonification (NH_4^+ -N production) was occurring, this was recorded at sub-zero temperatures (Fig. 7a). In Gl_{cryic} barley and grass soils, net ammonification occurred at -2 and -10 °C (Gl_{cryic} barley) and -10 °C (Gl_{cryic} grass) respectively. In Kor_{frigid} barley

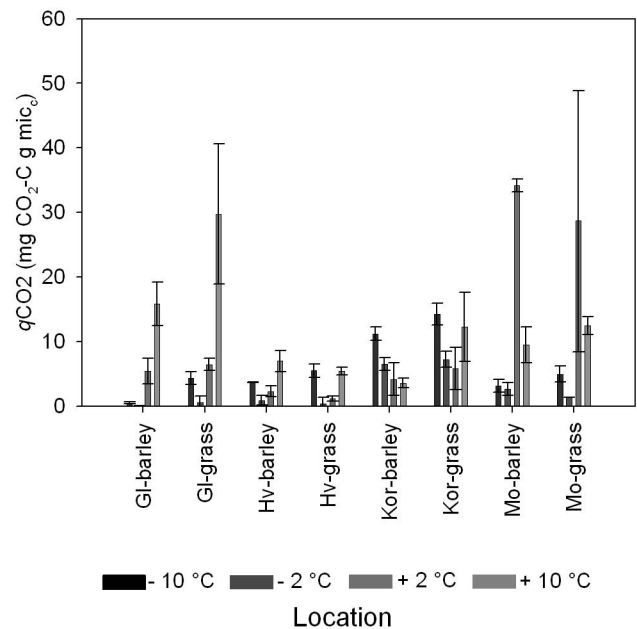


Fig. 4. qCO_2 for all soils, land use systems and soil temperature regime after 2 weeks incubation at -10 °C, -2 °C, $+2$ °C and $+10$ °C. Columns represent mean \pm 1 SE ($n = 3$). Gl=Glaumbær, Hv=Hvanneyri, Kor=Korpa, Mo=Möðruvellir.

and grass soils, net ammonification was occurring at -2 °C and -10 °C and -2 °C respectively (Fig. 7a).

Net nitrification (NO_3^- -N production) was site specific and independent of soil temperature regime or land use (Fig. 7b). For both Gl_{cryic} and Kor_{frigid} soil net nitrification was the dominant process at all temperatures with the exception of Gl_{cryic} grass which had net NO_3^- -N immobilisation at -10 °C and -2 °C. Net NO_3^- -N immobilisation was the dominant process in Hv_{frigid} and Mo_{cryic} soils. Gl_{cryic} barley and grass had net nitrification at -10 °C and -2 °C and -10 °C respectively.

Net N-mineralisation (NH_4^+ -N + NO_3^- -N), was also site specific (Fig. 7c) with no relationship with soil regime, land use or incubation temperature. No significant relationships were detected between site specific characteristics like C_{tot} , N_{tot} , C:N and soil pH.

4 Discussion

The physicochemical properties of the soils were similar to those that typified Andosols of Iceland (Arnalds, 2004). Temperature sensitivity of soils differed according to which temperature regime they were sampled from. Soils sampled from the frigid temperature regime experiencing less climatic extremes, were not sensitive to differences in temperatures. Lipson et al. (2000) and Sjurseth et al. (2005) reported that mic_c may be unaffected by single or multiple freeze-thaw events, particularly when the events are not extreme

Table 2. Q_{10} values for cumulative C_{\min} for the temperature ranges of -10°C to -2°C , -2°C to $+2^{\circ}\text{C}$ and $+2^{\circ}\text{C}$ to $+10^{\circ}\text{C}$ and dehydrogenase and arylphosphatase activity two weeks of incubation at the temperature ranges of -2°C to $+2^{\circ}\text{C}$ and $+2^{\circ}\text{C}$ to $+10^{\circ}\text{C}$. Q_{10} values are means of 3 replicates ($n = 3$).

Soil location and treatment	Cumulative CO_2			Dehydrogenase		Phosphatase	
	-10 to -2°C	-2 to $+2^{\circ}\text{C}$	$+2$ to $+10^{\circ}\text{C}$	-2 to $+2^{\circ}\text{C}$	$+2$ to $+10^{\circ}\text{C}$	-2 to $+2^{\circ}\text{C}$	$+2$ to $+10^{\circ}\text{C}$
Gl-barley, cryic	2.8	1.3	3.5	0.2	2.0	0.3	2.0
Gl-grass, cryic	1.9	1.5	2.7	3.4	1.5	1.6	1.1
Hv-barley, frigid	0.3	17.5	2.5	1.9	1.2	219	0.4
Hv-grass, frigid	1.3	4.6	1.9	0.7	1.8	11.9	0.6
Kor-barley, frigid	1.1	1.6	0.9	0.4	1.6	46.3	1.2
Kor-grass, frigid	1.7	0.6	0.8	3.4	1.1	647	1.2
Mo-barley, cryic	1.4	0.6	3.5	1.1	1.7	0.1	1.3
Mo-grass, cryic	0.8	4.3	1.5	0.3	1.8	12.1	1.3

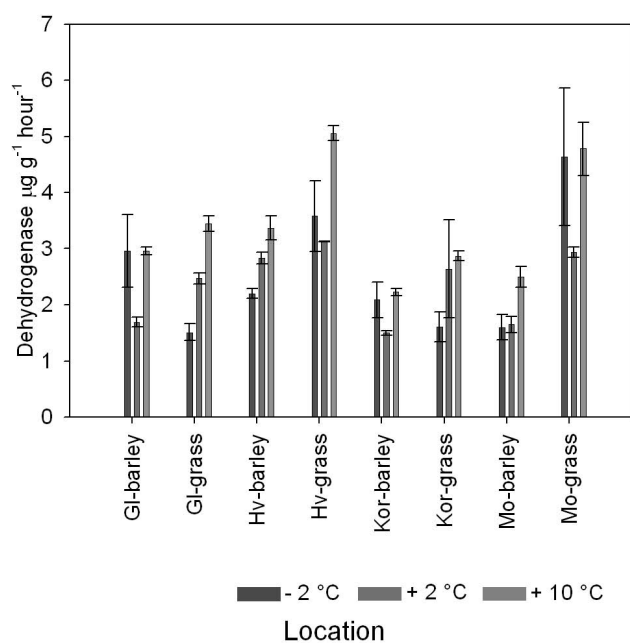


Fig. 5. Dehydrogenase activity for all soils, land use systems and soil temperature regime after 2 weeks incubation at -2°C , $+2^{\circ}\text{C}$ and $+10^{\circ}\text{C}$. Columns represent mean ± 1 SE ($n = 3$). Gl=Glaumbær, Hv=Hvanneyri, Kor=Korpa, Mo=Möðruvellir.

but frequent. This is likely to be the case in Iceland where temperatures within cultivated soils rarely drop below -5°C in lowland agricultural soils (The Icelandic Meteorological Office, unpublished observations). During such temperature fluctuations, microorganisms associated with the mic_c could readily assimilate substrates in the soil which would in turn enhance activity (Schimel and Clein, 1996; Lipson et al., 2000). Soils sampled from the cryic temperature regime showed on the other hand a different behaviour with an abrupt decline in mic_c at above zero ($+2^{\circ}\text{C}$ and $+10^{\circ}\text{C}$) (Fig. 2). Such results have been reported in the literature.

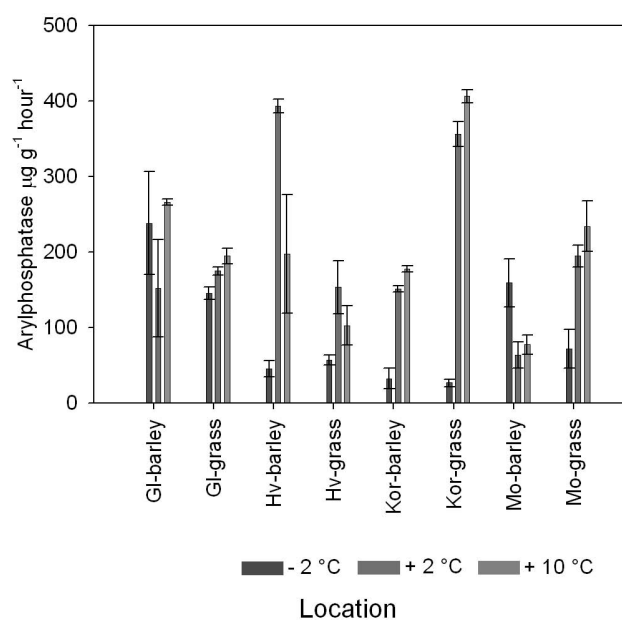


Fig. 6. Arylphosphatase activity for all soils, land use systems and soil temperature regime after 2 weeks incubation at -2°C , $+2^{\circ}\text{C}$ and $+10^{\circ}\text{C}$. Columns represent mean ± 1 SE ($n = 3$). Gl=Glaumbær, Hv=Hvanneyri, Kor=Korpa, Mo=Möðruvellir.

Lipson et al. (2000), Joergensen and Raubuch (2003) and Schimel and Mikan (2005) reported a decline in mic_c with increasing soil temperatures in arctic soils during laboratory incubations. Schimel and Mikan (2005) explained this decline to be the consequence of a substrate shift when temperature rise above 0°C as arctic soil spend a long time at or just below 0°C as they are freezing. The shift has been linked to depletion of available soil N due to soil warming (Edwards et al., 2006; Schimel and Mikan 2005). This was however not the case in this study as available NH_4^+ and NO_3^- was not sensitive to temperatures (Fig. 7a and b) nor was

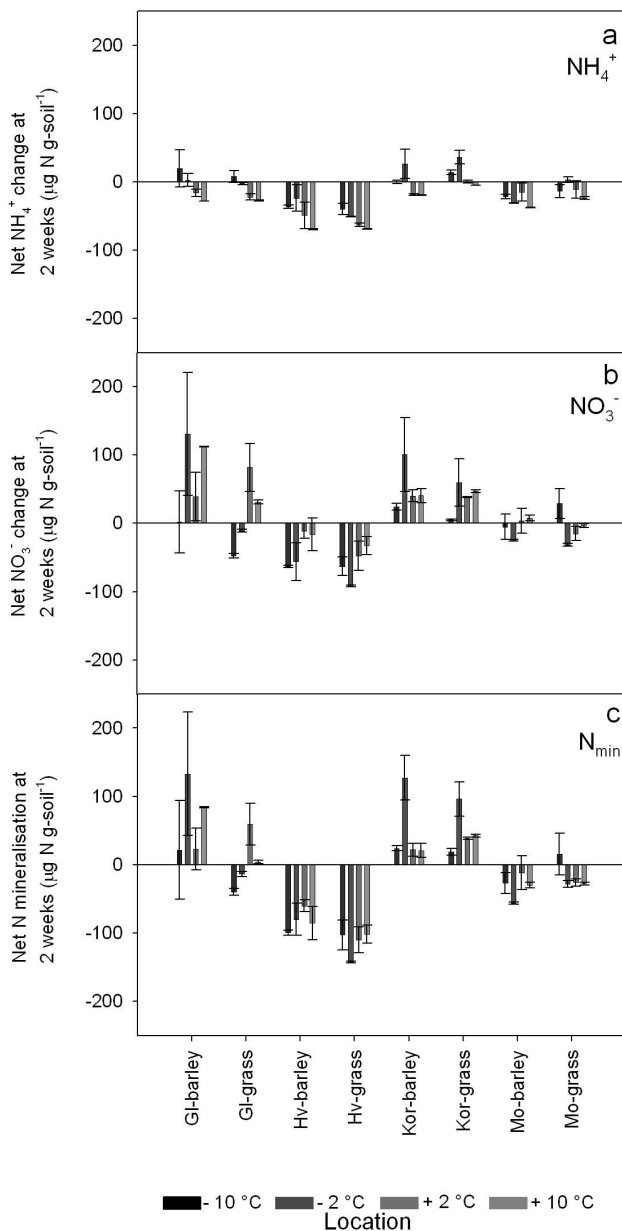


Fig. 7. Net Ammonification, nitrification and N_{\min} for all soils, land use systems and soil temperature regime after 2 weeks incubation at -10°C , -2°C , $+2^{\circ}\text{C}$ and $+10^{\circ}\text{C}$. Columns represent mean ± 1 SE ($n = 3$). Gl=Glaumbær, Hv=Hvanneyri, Kor=Korpa, Mo=Möðruvellir.

there a correlation with mic_c . Edwards et al. (2006) similarly reported a decreasing mic_c with rising temperatures during field measurements. Edwards et al. (2006) argued that a higher mic_c during colder temperatures was the result of lower microbial activity slowing down turnover rates. In this study lowest C_{\min} rates and enzymatic activity was measured at -10°C and highest at $+10^{\circ}\text{C}$ (Fig. 3 and Fig. 8). Another theory was presented by Lipson et al. (2000), which stated that although higher latitudes soil mic_c was resistant to fluctua-

tuations around 0°C the winter microbial community was sensitive to soil temperatures that remained above the freezing point. This is likely to have been the case with cryic soils from this study.

Measurements of C_{\min} (cumulative CO_2 over 2 weeks at -10°C , -2°C , $+2^{\circ}\text{C}$ and $+10^{\circ}\text{C}$) increased with warming reflecting temperature dependent soil heterotrophic activity (Fig. 3). Measurable C_{\min} at sub-zero temperatures has been widely reported in high arctic, arctic and sub-arctic soils and has mostly been attributed to unfrozen water films around soil particle. These are sufficient to maintain microbial activities even at low temperatures (e.g. Coxon and Parkinson 1987; Clein and Schimel 1995; Brooks et al., 1997; Mikan et al., 2002; Miller et al., 2007). Q_{10} values from soil temperature regimes of this study were comparable with Q_{10} values from sub-alpine organic soils (Q_{10} , 2.5) (Reichstein et al., 2000), alpine soils (Q_{10} , 2.5 to 3.8) (Fierer et al., 2006) and sub-Antarctic soils (Q_{10} , 1.8 to 2.5) (Smith, 2003), but generally lower than Arctic tundra soils (Q_{10} , 4.6 to 9.4) (Mikan et al., 2002). Although calculated Q_{10} values were highest in the range of -2°C to $+2^{\circ}\text{C}$, Q_{10} values in this study could not be related specifically to temperature treatment, soil temperature regime or landuse. Leifeld and Fuhrer (2005) found a negative relationship between Q_{10} values and CO_2 production when studying the temperature response of different soil fractions during a long term incubation experiment (707 days) and suggested that such a relationship was due to higher temperature sensitivity of lower SOM quality. No such relationship was found in this current study likely due to the fact that this was a short term experiment only measuring the labile fraction of the soil C as less than 1% of SOM was respired during the two week experiment. Connent et al., (2008) investigated the relationship between organic matter lability and temperature sensitivity and assumed that when 9–10% of the initial C had respired this was representative of the recalcitrant organic matter pool. This confirms the complexity of the soil environment when trying to draw conclusions from single measurements but it also highlights that nutrient cycling is maintained in cold environments (Koch et al., 2007). This is further confirmed when the $q\text{CO}_2$ values are considered as this could suggest that the microbial stress in relation to growth and maintenance was independent of the treatments (Killham, 1985).

Dehydrogenase and arylphosphatase activity were measured at sub-zero temperatures and this observation is in agreement with previous workers (Bremner and Zantua, 1975). The existence of unfrozen water films at sub-zero temperatures in Icelandic soils is likely due to the high relative water holding capacity and low bulk density associated with volcanic soils (Arnalds, 2004). Dehydrogenase activity correlated with the measured C_{\min} ($r = 0.86$, $P < 0.05$). Highest dehydrogenase enzyme activity was measured at the highest temperatures. The Q_{10} values were greater in the range of $+2^{\circ}\text{C}$ to $+10^{\circ}\text{C}$ compared to -2°C to $+2^{\circ}\text{C}$ and were generally below 2 (Table 2), indicating

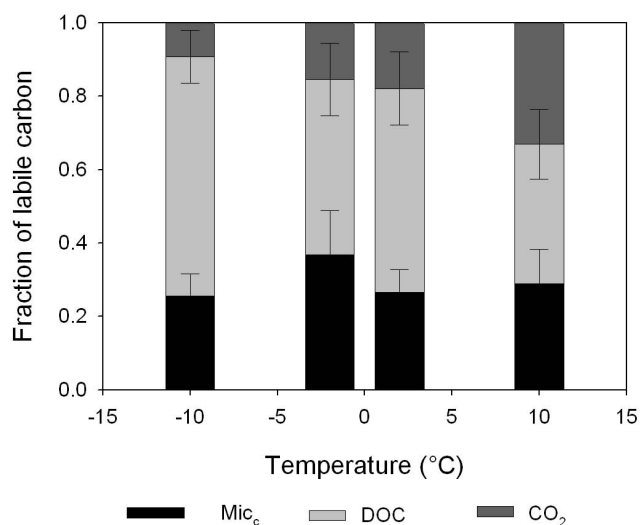


Fig. 8. Fractions of labile carbon for all soils, land use systems and soil temperature regime after 2 weeks incubation at -10°C , -2°C , $+2^{\circ}\text{C}$ and $+10^{\circ}\text{C}$. Columns represent mean ± 1 SE ($n = 3$).

that dehydrogenase activity was less temperature dependent within that range as previously reported (Browman and Tabatabai, 1978; Tabatabai, 1982).

Arylphosphatase activity has also been measured at sub-zero temperatures (Bremner and Zantua, 1975). The greatest arylphosphatase increase was observed between -2°C to $+2^{\circ}\text{C}$ rather than from $+2^{\circ}\text{C}$ to $+10^{\circ}\text{C}$, which had been the case for dehydrogenase activity. As a consequence, arylphosphatase activity coefficients (Q_{10}) were higher in the range -2°C – $+2^{\circ}\text{C}$ compared to $+2^{\circ}\text{C}$ – $+10^{\circ}\text{C}$ (Table 2). Arylphosphatase activity was more sensitive to temperature around the freezing point than dehydrogenase activity (Browman and Tabatabai 1978).

When all carbon pools, mic_c , DOC and C_{min} have been combined (Fig. 8), a pattern is revealed. The biomass pool remains constant throughout all temperature treatments, but as temperature rises there is a commensurate rise in respiration because the DOC pool is being metabolised. This results in lower DOC concentrations when soil respiration is highest and corresponding highest measured DOC concentrations when respiration is lowest (Fig. 8). No difference was observed in all three carbon pools at temperatures in the range -2°C and $+2^{\circ}\text{C}$ (Fig. 8), hence the soils have been conditioned to perform around these temperatures. The soils of Iceland experience unusually frequent freeze and thaw cycles, indeed more than any other sub-arctic region (Orradottir 2002). Hence it would be expected that the soils would be adapted to such critical temperatures.

At -10°C , DOC accounted for 88% of the total measured C released (respiration + DOC), but at $+10^{\circ}\text{C}$ this was only 65%. This response is similar to the temperature dependent observations of Miller et al. (2007) in sub-arctic soils. Hob-

bie et al. (2000) stated that cold season respiration may be mediated by DOC and that this in turn would regulate microbial biomass size and activity. It has been reported that during the cold season, microbial biomass switches from processing plant detritus and SOM to relying more heavily on recycled microbial biomass and dissolved organic matter (DOM) in unfrozen water films (Schimel and Mikan, 2005; Sharma et al., 2006). These results confirm the conservative microbial dynamics of such soils and highlight that DOC is a major component of C released in the coldest temperature treatment (-10°C) while CO_2 is the major component of C release at the highest temperature. This highlights the strong temperature dependency of DOC and the close link between soil DOC and soil microbial activity in Icelandic soils. It should though be noted that the DOC pool contains a complex mix of C compounds with some being a complex of C compounds, some of which are more labile and will cycle fast while other might be more recalcitrant (Schimel and Mikan, 2005; Boddy et al., 2008). It has also been discussed that the more resistant fraction of DOC might have different temperature dependencies than the more labile fraction (Knorr et al., 2005; Bauer et al., 2008). Soil warming experiments have demonstrated that increased carbon efflux rates by increasing temperatures returns eventually to similar rates as before the temperature increase. This was believed to demonstrate that the response pattern was not due to acclimation response of soil microorganisms but due to depletion of readily decomposable substrate (Davidson et al., 2000; Ågren and Bosatta, 2002; Kirschbaum, 2004; Bauer et al., 2008). This study was conducted on a short time scale (2 weeks) and measured the initial breakdown of the labile fraction of DOC and it can not be excluded that if the experiment would have been conducted on a larger time scale that the response pattern would have yielded different carbon efflux rates. It is however believed that availability of labile C compounds may be a major component in controlling soil respiration of high latitude systems (Boddy et al., 2008) and studying the short term response of the more labile fraction of DOC merits investigation.

In terms of the nitrogen dynamics, the system behaves in a more complex way than authors have reported for soils of the high Arctic (Schimel and Clein, 1996; Schimel and Mikan, 2005) and sub-arctic (Miller et al., 2007). This is not surprising as despite Iceland's high latitude, these soils are productively cultivated. The soils are more mature than soils in the high arctic with a significantly larger microbial biomass, greater concentration of labile carbon and considerably more C_{min} . In each of the soils studied there was evidence of considerable ammonification as temperatures rose from -10°C . N_{min} occurred in certain soils simultaneously both above and below the freezing point which is consistent with previous studies in the arctic and sub-arctic (e.g., Schimel and Clein, 1996; Schimel and Mikan, 2005; Oquist et al., 2004; Miller et al., 2007). There is little doubt that ammonification is more active as the temperature rises but so is the immobilisation of

resultant NH_4^+ as activity per unit of microbial biomass increases. The resultant NH_4^+ -N in the soils is being utilised by the microbial biomass, and this can be seen by the close correlation between C_{\min} (cumulative CO_2) and soil NH_4^+ -N concentration (Fig. 9). At the highest NH_4^+ -N concentrations, there is the lowest cumulative respiration (C_{\min}) while those soils with highest microbial activity have negligible NH_4^+ -N, suggesting the N limitation of these soils. These results are in agreement with other studies of sub-arctic soils that acknowledge that NH_4^+ -N production is temperature dependent and enhanced during thawed conditions (Muller et al., 2002; Miller et al., 2007). Hobbie and Chapin (1996) suggested that N limitation in arctic soils was due to decomposing litter during the cold season, while Weintraub and Schimel (2003) and Schimel et al. (2004) stated that these ecosystems were fundamentally N limited. These results support the findings of Palmasson et al. (1996) and Gudmundsson et al. (2004) that N is the constraining factor in Icelandic soils. Nitrogen limitation in these soils has been attributed to three main factors (Ritter, 2007): Andic soil properties which slow down organic N turnover, low N mineralisation rates (Palmason et al., 1996) and low atmospheric N deposition (Ritter, 2007). Overall N_{\min} was not temperature dependant nor was there an association with soil temperature regimes or landuse suggesting that cryic and frigid soils was likely determined by site specific aspects such as microbial biomass composition rather than temperature. Koch et al. (2007) and Wallenstein et al. (2008) reported that N degrading enzymes tend to be less sensitive temperatures than C degrading enzymes displaying generally lower Q_{10} values. It may be further considered that N_{\min} in Icelandic soils will be little affected with increasing temperatures in the Arctic but rather controlled by soil microbial activity and composition as well as substrate form and availability (Koch et al., 2007).

The soils for this study were selected to reflect managed Icelandic land uses in different temperature regimes. It is acknowledged that they have a considerable carbon binding capacity and the release of carbon from these environments as a consequence of climate change could have significant global impacts. While these soils may have evolved to become conditioned to continual freeze-thaw episodes elevated temperatures could alter the labile C pool in the short term. Soil climatic conditions seem to have an impact on Icelandic soil mic_c with soils sampled from the cryic temperature displaying more sensitivity to increasing temperatures than soils experiencing a less harsh climate (frigid temperature regime).

5 Conclusions

Microbial biomass size from frigid temperature regimes was not affected by temperature above and below the freezing point in the short term, but the resultant activity was. By selecting a range of activity measurements a better under-

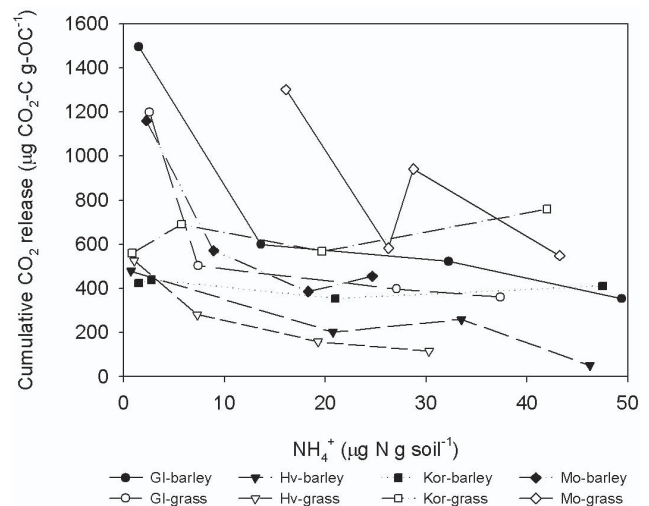


Fig. 9. C_{\min} (cumulative CO_2 release) versus ammonium for all soils, land use systems and soil temperature regime after 2 weeks incubation -10°C , -2°C , $+2^\circ\text{C}$ and $+10^\circ\text{C}$. Columns represent mean ± 1 SE ($n = 3$). GI=Glaumbær, Hv=Hvanneyri, Kor=Korpa, Mo=Möðruvellir.

standing of the dynamics can be developed. In this study, nitrogen dynamics seemed to reflect site specific criteria rather than temperature treatments. The response of labile carbon in these soils was governed by temperature and there is a careful balance between DOC and carbon mineralisation.

Acknowledgements. We thank the Icelandic Governmental Fund for Graduate Education and The Agricultural Productivity Fund for funding this work.

Edited by: H. Lankreijer

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