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Temperature response of soil organic matter mineralisation in arctic soil profiles

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Covering Letter

Dear Editor

Please find attached a manuscript entitled: "Temperature sensitivity of soil organic matter mineralisation in the arctic".

We think that Soil Biology and Biochemistry is the right format for publishing this article which combine SOM dynamic composition and microbial community structure investigation. In addition, this work was conducted on permafrost soils which are highly important for climate change!

Looking forward to hearing from you.

Best regards,

Christophe

Dear editor,

Please find attached the revised version of the manuscript "SBB9781R1".

As suggested in the main remaining comment of the reviewer, we have decided to reanalyze the Q10 data following a procedure in line with the reviewer's suggestion. Interestingly, this has actually led to somewhat different conclusions regarding this particular section. We agree with the reviewer that this way to analyze the data is more appropriate than the cumulative approach used before. We have rewritten the related discussion accordingly. We have also emphasized the (unchanged) results on intensity of mineralization, as asked by the reviewer.

We have fully followed through the suggestions and comments of the reviewer and hope that this will allow for publication in Soil Biology and Biochemistry

Sincerely yours,

Christophe Moni and co-authors

Detailed answer

"I welcome that the term "temperature sensitivity" was removed from the title. However, the description "Early temperature response of soil organic matter mineralisation" is not easy to understand. I would prefer the term "mineralisation intensities" of SOM and I propose to add in the title that different soil layers were examined."

The title of the manuscript was modified to satisfy both the suggestion of the reviewer and the revised manuscript content.

We now propose the following title: "Temperature response of soil organic matter mineralisation in arctic soil profiles"

We maintained the term "temperature response" instead of the suggested "mineralization intensities" as our term encompass both intensity of mineralization and temperature sensitivity. However in this new version of the manuscript the intensity of mineralization is preponderant compared to the temperature sensitivity, while temperature sensitivity was re-estimated according to a method in line with the suggestions of the reviewer.

To indicate that different soil layer were examined we precised that soil profiles were examined.

As stated in my first review I question that temperature sensitivity can be estimated correctly by summing up CO₂ production over 91-day incubations at different temperatures. Unfortunately the authors don't cite literature to explain the basics of their method used and to compare their results with similar examinations. This should be done in a revised version.

The carbon mineralisation rates that are presented in Figure S1 clearly show that SOM of increasing stability is mineralized during the incubation period. Some soils show strong mineralization flushes at the beginning of the incubation and strong declines in their mineralization rates thereafter - other soils do not show that dynamics. This result clearly demonstrates that pools of different stability are mineralized to different degrees in the different soils. Further, respiration rates decline faster at higher temperatures with faster depletion of substrates. Temperature sensitivity normally is measured in laboratory incubations by using short-term temperature manipulations (max. 24h) at different (defined) stages during SOM mineralisation e.g. during and after depletion of the active pool. By summing up the cumulative CO₂ respiration over a 91-day incubation period there is no way to know how pool sizes of active and passive SOM fractions changed and a mechanistic evaluation of the soil respiration-temperature relationships is not possible. Further it is not possible to draw clear statements and logical conclusions.

It doesn't matter that the authors cannot specify the mechanisms behind. The point is that the authors always should provide clear information on the validity, significance and the limitations of their methods used and that they should discuss their results against this background.

I acknowledge, that the authors included in their revised text and in their interpretations that their Q10-estimates integrate fast and slow pools. The discussion is now better and even coherent.

In recognition of the concerns mentioned above, I still propose to focus the manuscript on the carbon mineralization intensities and to include in more detail in results and discussion the mineralisation rates that are presented in Figure S1 (see also specific comments). This information is essential to correctly interpret the obtained results, to categorize them more easily and to verify them scientifically.

To focus on carbon mineralization intensities and mineralization rates, the manuscript was completely reworked

Mineralization rates that were previously displayed in the supplementary information are now displayed in the main list of Figure. On the contrary, the exponential model fits are now displayed in the supplementary information.

Mineralization rates are now discussed in one full section of the discussion, whereas Intensity of mineralization estimated from the whole incubation period (old analysis) and at the end of the incubation period (new analysis) are more thoroughly discussed in another section of the discussion. To eliminate the effect of the fast cycling pool on the temperature sensitivity estimation, Q10s were estimated from the CO₂ data obtained on the last step of incubation after the initial flush of mineralization had passed.

Our new approach was redefined in the material and methods section and supported by literature references.

Table 3 presenting a synthesis of Q10 values for permafrost-affected soils was expanded to enable a better comparison with our results.

Specific comments:

1. Line 22: focus on mineralization intensity, please. "Here, we investigate the mineralization intensity..."

In the following sentence: "Here, we investigated the temperature sensitivity response of SOM mineralization "we replaced "temperature sensitivity response" by "temperature response" which encompass both the intensity of mineralization and the temperature sensitivity of SOM mineralization.

2. In the new Chapter 2.5.1 "Choice of method" the authors state, that their choice was guided by "(3) ease of comparison of the estimators with those obtained in other studies". Please add references!

Our method was modified, and the "choice of method" section was completely rewritten.

3. Chapter 2.5.1: Please add also the constraints of the method used (see above)! This information is very important for the reader who is planning similar examinations. Temperature sensitivity normally is measured in laboratory incubations by using short-term temperature manipulations (max. 24h) at different stages during SOM mineralisation.

Again, our method was rewritten and a short discussion was included about the limitation of the method.

3. Line 177-179: "In our samples... which reduces the impact of the one-pool-model artefacts on apparent Q10". I do not understand this sentence. Please explain the reasons why the exhaustion of the active pool (in some soils) reduces the impact of the one-pool-model artefacts on apparent Q10. What exactly is an "apparent" Q10? Figure S1 clearly shows, that pools of different stability are mineralized to different degrees in the different soils.

As the Q10 estimation method has changed this comment is no longer relevant.

4. Line 225: "Considering permafrost affected soils, the proportion of mineralized OC was always significantly higher in deep layers". Add information from Fig. S1 on the pools that are mineralized. The mineralization rates in Fig. S1 clearly demonstrate in which soils and soil layers pools of different stability are mineralized.

There is now a full analysis of the mineralization rate covering this point in the discussion section.

5. Chapter 2.5.2: add references please!

References for studies using the exponential model were added in the next section.

6. Line 219: add Table 1

Reference to Table 1 added.

7. Line 469: add pages

Pages added, although the pages format was unusual.

9. Line 525: Please format references uniformly according to guidelines of Soil Biology and Biochemistry

We had used the Endnote template provided by SBB to format our previous list of reference. So it should have been uniformly formatted. A new reference list was generated using the same template and we hope that everything is in order now.

Highlights

- Temperature response of SOM mineralization studied in profiles for 3 Arctic sites
- Initial mineralization intensity higher in permafrost than active layers
- Uniform Q10 among samples (1.21 to 1.43)
- OM composition and microbial community structure site specific, not depth related
- OM and microbes not directly linked to mineralization intensity and Q10

1 **Temperature response of soil organic matter mineralisation in arctic soil**
2 **profiles**

3

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15

16 Keywords: arctic peat soil, permafrost, mineralisation, temperature sensitivity, soil organic matter, soil
17 microbial communities

18 **Abstract**

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Soil organic matter (SOM) in arctic and boreal soils is the largest terrestrial reservoir of carbon. Increased SOM mineralisation under increased temperature has the potential to induce a massive release of CO₂. Precise parameterisation of the response of arctic soils to increased temperatures is therefore crucial for correctly simulating our future climate. Here, we investigated the temperature response of SOM mineralisation in eight arctic soil profiles of Norway, Svalbard and Russia. Samples were collected at two depths from both mineral and organic soils, which were affected or not by permafrost and were incubated for 91 days at 4, 8, 12, and 16 °C. Temperature response was investigated through two parameters derived from a simple exponential model: the intensity of mineralisation, α , and the temperature sensitivity, Q₁₀. For each sample, SOM quality was investigated by ¹³C-NMR, whereas bacterial and fungal community structure was characterised by T-RFLP and ARISA fingerprints, respectively. When estimated from the whole incubation period, α proved to be higher in deep permafrost samples than in shallow active layer ones due to the presence transient flushes of mineralisation in deep permafrost affected soils. At the end of the incubation period, after mineralization flushes had passed, neither α nor Q₁₀ (averaging 1.28 ± 0.07) seemed to be affected by soil type (organic vs mineral soil), site, depth or permafrost. SOM composition and microbial community structure on the contrary were affected by site and soil type. Our results suggest that deep samples of permafrost affected soil contain a small pool of fast cycling carbon, which is quickly depleted after thawing. Once the mineralization flush had passed, the temperature response of permafrost affected soil proved to be relatively homogenous among sample types, suggesting that the use of a single temperature sensitivity parameter in land surface models for SOM decomposition in permafrost-affected soils is justified.

45 **1 Introduction**

46 Arctic and boreal soils from the northern circumpolar permafrost region represents more than half of the
47 global soil organic matter (SOM) (Jobbagy and Jackson, 2000; Tarnocai et al., 2009). Most global
48 circulation models tend to predict a 1-3.5 °C increase in mean global surface temperature by the end of
49 the century with a disproportional increase at high latitudes (Houghton et al., 1996; Räisänen et al.,
50 2004). This increase in temperature may accelerate the decomposition of SOM in high latitude regions,
51 thereby generating large emissions of greenhouse gases (GHG) and a positive feedback on the global
52 temperature (Friedlingstein et al., 2006). Therefore, characterising the intensity of SOM mineralization
53 after thawing and its sensitivity to temperature increase is crucial for predicting the evolution of the
54 Earth's climate. The response of SOM decomposition to increasing temperature, hereafter referred to as
55 SOM temperature sensitivity, appears complex because it results from the interaction of multiple factors
56 and mechanisms (von Lützow and Kögel-Knabner, 2009). Indeed, substrate quality (e.g. Feng and
57 Simpson, 2008; Frey et al., 2013, Kätterer et al., 1998), substrate availability (e.g. Fissore et al., 2013;
58 Gershenson et al., 2009; Gu et al., 2004; Bengtson and Bengtsson, 2007), microbial community structure
59 and functioning (Wei et al., 2014), as well as environmental factors (Conant et al., 2011) have been
60 shown to govern temperature sensitivities of both SOM mineralisation rates and C use efficiency. Arctic
61 soils have been reported to display contrasting properties as compared to more temperate soils, including
62 SOM and microbial community compositions. In particular, arctic permafrost soils are rich in soluble
63 compounds and cellulose, which could decompose easily under warmer conditions (Michaelson et al.,
64 2004). SOM physically protected in ice clogged aggregates within permafrost layers is in particular
65 expected to become suddenly available after thawing. However, despite the importance of arctic soils,
66 little is known about the dynamic of their organic matter (OM) stocks and their response to global
67 warming (McGuire et al., 2009; Schmidt et al., 2011).

68 The objectives of the present study are to characterise through laboratory incubations the mineralisation
69 responses of arctic soils to increasing temperature immediately after the thawing, and to further identify
70 potential relationships with SOM composition and microbial community structure. Here, we hypothesise
71 that SOM temperature response in arctic and permafrost affected soils is controlled by environmental
72 factors such as the presence or absence of permafrost, the prevailing organic vs. mineral nature of the soil
73 (hereafter functionally referred to as “soil type”) and soil depth.

74

75 **2 Material and methods**

76

77 **2.1 Soil sampling and physico-chemical characterisation**

78 Eight soil profiles in total were sampled in Adventdalen (A) in Svalbard, Vorkuta (V) in North-Western
79 Russia, and Neiden (N) in Finnmark (Norway). The A1 and A2 profiles are permafrost affected, and
80 according to the last version of the World reference base for soil resources (IUSS Working Group WRB,
81 2014) are classified as non-cryoturbated Haplic Cryosols. The V1 and V4 profiles are permafrost affected
82 and cryoturbated mineral soils, classified as Turbic Cryosols. The V2 profile is a non-permafrost non-
83 cryoturbated mineral soil, classified as Gelistagnic Cambisol, and V3 is a permafrost affected peat soil
84 belonging to the Cryic Histosol. Palsas are dynamic ice-core peat mounds occurring in polar and subpolar
85 climates, whose genesis and features are well described in Seppälä (1986). The N1 profile is permafrost
86 affected palsa peat classified as Cryic Histosol, and N2 is an adjacent non-permafrost peat soil classified
87 as Hemic Histosol. Soil sampling was conducted between July and September 2008. Profiles were dug in
88 the non-frozen soil and, when applicable, cylindrical cores were drilled or hammered into the permafrost
89 layer. Two large (1-3 kg) bulk samples were taken from each soil profile at two depths, shallow (suffix s)
90 and deep (suffix d), the depths depending on the sampling site (Table 1). In fact, care was taken to avoid
91 the surface soil and the transition zone between active and permafrost layers. For ease of following
92 sample properties, a two-letter descriptor was added to each sample identifier using “A”, “P”, “O”, “M”
93 for “Active layer”, “Permafrost layer”, “Mineral soil” and “Organic soil”. As an example, the following
94 denomination, V4d_(PM), designates the sample taken at the bottom of the fourth profile sampled at
95 Vorkuta and indicates that this sample is a permafrost affected mineral soil. All soil samples were kept
96 frozen at -18 °C immediately after sampling until analysis. Aerobic incubations were conducted on field-
97 moist samples, i.e. the soils were never allowed to completely dry out. Frozen soil samples were thawed
98 on filter paper in a 10°C controlled room and left for 72 hours to drain. Aliquots of these samples were
99 taken for soil analyses. Soil pH was measured in deionised water (1:2.5) with a combined Orion pH
100 electrode (SA 720, Allometrics, Inc., Baton Rouge, LA). Soil gravimetric moisture contents were
101 estimated with oven drying at 105°C for 48 hours. Total C and N were determined by dry combustion
102 using a LECO[®] CNH1000 analyser. The results were used to recalculate the initial amount of dry soil and

103 total C in the incubated samples (Table 1).

104

105 **2.2 Carbon mineralisation measurement**

106 Moist samples at field capacity of mineral and organic soil, 50 and 20 g respectively, were incubated in
107 triplicates in 250-ml serum vials. Prior to capping with CO₂-tight butyl-rubber stoppers, vials were
108 flushed with compressed air. Thorough flushing of the vials containing the soil samples was controlled
109 with an infra-red gas analyser (IRGA) (EGM-4 PP System, Amesbury, MA, USA). Flushing time of one
110 minute proved to be sufficient to reach the CO₂ concentration of compressed air, i.e. 147 ± 2 ppm. Butyl-
111 rubber stoppers were partially inserted before removing the flushing tube, so that end of flushing and
112 capping were simultaneous. Serum vials were placed in triplicates in incubators in the dark for 91 days at
113 4, 8, 12, and 16 °C. Moisture content was kept constant during the course of the entire incubation period
114 by weighing each sample and spraying distilled water to compensate for any water loss. Measurements of
115 soil C mineralisation were performed at approximately two-week intervals over a 91-day period. Carbon
116 mineralisation rates were determined by measuring the accumulated CO₂ concentration in the vial
117 headspace. Measurements were performed with a micro gas chromatograph (Agilent 3000 Micro-GC,
118 France). Samples were flushed and recapped at intervals that prevented the headspace CO₂ concentration
119 to ever exceed 35000 ppm, the value at which anaerobic thresholds have been reported (MacFadye,
120 1973). Samples were capped between 4 and 14 days before measurements.

121

122 **2.3 Analysis of soil organic matter by ¹³C-CPMAS NMR**

123 Solid-state ¹³C-CPMAS NMR spectra were recorded on a Bruker AMX 300-WB spectrometer equipped
124 with a 4 mm CPMAS probe. Experimental conditions were: 90° pulse = 3.1 μs, contact time = 3 ms,
125 relaxation delay = 3s, spinning rate = 8 kHz, and number of scans between 8,000 and 32,000 depending
126 on the SOM content of the sample. The soil samples were indirectly enriched in C selectively removing
127 single sand grains by hand-picking under a 20x lens. Then they were treated with 2% hydrofluoric acid as
128 in Skjemstad et al. (1994) to remove paramagnetic materials, which give rise to broadened resonances
129 and signal loss. The combined mechanical and chemical treatments for preparing soil samples for the
130 NMR analysis increased the C concentration in the Adventdalen and Vorkuta samples by 80 to 220%,
131 which allowed high quality spectra to be obtained, except for the non-frozen deep layer of V2_(AM), which,

132 despite the treatments, had a too low C content. A semi-quantitative estimation of the main C forms was
133 obtained by integrating five chemical shift regions (0-45 ppm, alkyl C; 45-110 ppm, O-alkyl C; 110-165
134 ppm, aryl C; 165-185 ppm, carboxyl C; 185-220 ppm, carbonyl C) and expressing them as percentages of
135 the total spectral intensity; where observed, the contribution of rotational sidebands, often observed for
136 aryl and carbonyl/carboxyl resonances, was taken into account (Smernik et al., 2008)

137

138 **2.4 Microbial communities profiling**

139 Bacterial and fungal communities were analysed using a Terminal restriction fragment length
140 polymorphism (T-RFLP; Osborn et al., 2000) and automated ribosomal intergenic spacer analysis
141 (ARISA; Ranjard et al., 2003), respectively. The DNA was extracted from 0.25 g of soil using the
142 FastDNA™ SPIN Kit for Soil (MP Biomedicals) according to the manufacturer's instructions. Bacterial
143 16S rRNA gene was amplified using primers 63F (5'-CAGGCCTAACACATGCAAGTC-3')
144 fluorescently labelled at the 5' end with FAM dye and 1389R (5'-ACGGGCGGTGTGTACAAG-3')
145 (Marchesi et al., 1998). Fungal internal transcribed spacers (ITS) were amplified, using the primers
146 ITS1F (5'-CTTGGTCATTTAGAGGAAGTAA-3') (Gardes and Bruns, 1993) fluorescently labelled at
147 the 5' end with Yakima Yellow® dye and ITS4 (5'-TCCTCCGCTTATTGATATGC). PCR were
148 performed with 2µL of diluted (1:10) DNA template in a total volume of 20µL (Master Mix Kit, Qiagen)
149 and 0.05 mM of each primer. Biorad T100 thermal cycler was used for the amplification with the
150 following programmes for T-RFLP: initial denaturation at 94 °C for 2 min, followed by 30 cycles of 94
151 °C for 30 s, 57 °C for 45 s, and 72 °C for 90 s, followed by a final extension time at 72 °C for 10 min. For
152 ARISA, PCR conditions consisted of an initial denaturation at 95 °C for 5 min, followed by 35 cycles of
153 95 °C for 30 s, 55 °C for 30 s, and 72 °C for 60 s, followed by a final extension time at 72 °C for 10.
154 Bacterial PCR products (10 µl) were digested with 10 U of the restriction enzyme AluI and 1× restriction
155 enzyme buffer (Thermo Fisher) in a total volume of 15 µl at 37 °C for 3 h. After a desalting step, 2µl of
156 PCR products were mixed with formamide containing 0.5% of ROX-labelled GS500 (T-RFLP) or
157 GS2500 (ARISA) internal size standard (Applied Biosystems,) in a total volume of 12 µl and denatured
158 at 94 °C for 3 min. Samples were electrophoresed on an ABI 3730 PRISM® capillary DNA sequencer
159 (Applied Biosystems). The T-RFLP and ARISA profiles obtained with the sequencer were analysed
160 using GeneMapper® v3.7 software (Applied Biosystems). The fragments between 50 and 500 bp and

161 peaks height ≥ 50 fluorescence units were included in T-RFLP analysis and Amplicons between 200 and
162 1500 bp and peaks height ≥ 100 fluorescence units were included for ARISA analysis. Fragments having
163 a relative abundance of proportion $< 0.5\%$ were removed from the matrices.

164

165 **2.5 Temperature sensitivity**

166 **2.5.1 Choice of method**

167 Multiple methods exist for estimating a temperature response from parallel soil incubations conducted at
168 different temperatures. The simplest one is the traditional one-pool exponential model, which fitted to
169 cumulated or instantaneous data, yields one conventional “Q10” parameter for temperature sensitivity
170 and one parameter for mineralization intensity. However, due to the differential exhaustion of C substrate
171 incubated at different temperature, the Q10 is generally underestimated when derived from long term
172 incubation cumulated data. In addition, this method does not take into consideration the composite nature
173 of SOM that can encompass several pools of OM with different stability. To circumvent this limitation
174 temperature sensitivity is normally measured in laboratory incubations by using short-term temperature
175 manipulations at different stages during SOM mineralisation e.g. during and after depletion of the active
176 pool (e.g. Conant et al., 2008; Hartley and Ineson, 2008). Once the active pool is depleted, the
177 temperature sensitivity underestimation becomes usually negligible and much less sensitive to the
178 duration of the temperature manipulation. Therefore, in our study, the long-term temperature sensitivity
179 was derived from the last incubation date, which was after the initial peak of mineralisation had passed,
180 and thereby ensured negligible distortions of the Q10. With respect to the mineralization intensity, we
181 were interested in investigating the response of SOM mineralisation just after the thawing. Therefore, we
182 derived it both from the cumulated quantity of organic carbon (OC) mineralised after 91 days of
183 incubation and from that collected during the last incubation step.

184 **2.5.2 Calculation**

185 We used an exponential function (e.g. Gershenson et al., 2009; Jenkins et al., 2011; Mikan et al., 2002;
186 Sierra et al., 2011; Wang et al., 2014) to describe the temperature dependence of OC mineralisation:

$$187 \quad C_{cum} = \alpha e^{\beta T} \quad (1)$$

188 where C_{cum} represents the cumulated quantity of OC mineralised either after 91 days of incubation or
189 during the last step of incubation (i.e. between 84 and 91 days) at temperature T relatively to the quantity
190 of soil organic carbon (SOC) present in the sample at the beginning of the incubation (mg C g^{-1} SOC), α
191 is the basal cumulated quantity of mineralised OC of incubation at 0°C and also represents the intensity of
192 the mineralisation, T is the incubation temperature in ($^\circ\text{C}$) and β is a parameter that describes the
193 temperature sensitivity of C . The traditional temperature sensitivity index Q_{10} (i.e. increase of CO_2
194 emission or carbon mineralisation for a 10°C increase in temperature) was derived from the following
195 equation:

$$196 \quad Q_{10} = e^{10\beta} \quad (2)$$

197 Mean cumulative respiration data were then fitted to equation (1) to obtain the best fit for α and β values,
198 and the parameter Q_{10} was calculated using equation (2).

199

200 **2.7 Statistical analysis**

201 All mineralisation curves were fitted using nonlinear procedures allowing for weighting (nls function) of
202 the R software (R 2.13.1©2011 The R foundation for statistical computing). Data point weight was
203 inversely proportional to SD. Parameters of SOM temperature sensitivity responses were analysed as a
204 function of sample location, depth, frost regime and soil type. Significant difference between groups were
205 tested using: (a) T test (two groups), (b) Paired T test (two groups of paired samples) and (c) ANOVA (>
206 two groups). When normality and equal variances conditions were not reached significant differences
207 were tested using non-parametric test: (d) Mann-Whitney Rank Sum Test (two groups), (e) Wilcoxon
208 signed rank test (two groups of paired samples), and (f) Kruskal-Wallis ANOVA on rank (> two groups).
209 Dunn or Holm-Sidak multiple comparison tests (with 95% confidence limits) were further used to test for
210 differences between sample categories. Fisher exact test was used to identify significant association
211 within contingency tables. Tests a, b, c, d, e, f and Fisher exact test were performed using the SigmaPlot
212 software (SigmaPlot 11.0 © 2008 Systat Software, Inc.). SOM composition and microbial communities
213 structure of each sample were compared by correspondence analysis (CA) using the proportion of NMR
214 functional groups (Alkyl C, O-alkyl C, Aryl C, Carboxyl C, Ketonic/Aldehydic C) and the relative

215 abundance of genetic fragments (TRFLP and ARISA matrices), respectively. Redundancy analyses
216 (RDA) were further performed to explore the relationships between microbial communities and soil
217 chemical properties. All multivariate analyses were performed using the “ade4TkGUI” package in R
218 while graphic representations were performed with SigmaPlot 11.0.

219

220 **3 Results**

221 The measured pH values of the investigated soils were all (except in V4d_(PM)) below neutrality (Table 1),
222 which leads to exclude the presence of carbonates and, as a consequence, their contribution to CO₂
223 emission during the incubation measurements (Tamir et al., 2011; Ramnarine et al., 2012). Mineralisation
224 rate ranged between 0.05 and 387.34 $\mu\text{g C g}^{-1} \text{SOC d}^{-1}$ and averaged $28 \pm 43 \mu\text{g C g}^{-1} \text{SOC d}^{-1}$ (Fig. 1)
225 At the end of the 91-day incubation period the proportion of mineralised OC averaged 2.2 ± 1.5 ; $3.6 \pm$
226 2.5 ; 5.4 ± 3.2 and $7.1 \pm 4.1 \text{ mg.g}^{-1}$ at 4, 8, 12, and 16 °C, respectively (Fig. S1). For all soil profiles but
227 V2_(AM), the proportion of mineralised OC at the end of the incubation period was significantly higher in
228 the deep soil samples than in the shallow ones. Considering permafrost-affected profiles only, the
229 proportion of mineralised OC was always significantly higher in the deep permafrost layer than in the
230 shallow active layer. Instantaneous mineralisation rate recorded over the 91-day incubation period (Fig.
231 1) clearly showed that SOM of increasing stability is mineralized during the incubation period. Three
232 different patterns were observed. While some samples experienced a strong initial mineralisation flush at
233 the beginning of the incubation period followed by a strong decline of the mineralisation rate (i.e A2d_(PM),
234 N2d_(AO), V1d_(PM), V2d_(AM), V4d_(PM)), others displayed rather stable mineralisation rate in time with no, or,
235 almost no, initial mineralisation flush (i.e. A1s_(AM), A2s_(AM), N1s_(AO), N1d_(PO), N2s_(AO), V3s_(AO), V1s_(AM),
236 V2s_(AM), V4s_(AM)). Finally two samples, A1d_(pm) and V3d_(po), presented a strong and sharp transient
237 increase of mineralisation rate that declined faster at higher temperatures with faster depletion of
238 substrates. Fisher exact test, showed that strong mineralisation flushes, initial or delayed, were
239 significantly associated to deep samples ($p = 0.001$) and to a lesser extent to permafrost samples ($p =$
240 0.035), while the distribution of the strong and weak mineralisation flush within soil types (i.e organic vs.
241 mineral) did not diverge significantly from a random distribution. For all soils, with maybe the exception
242 of A2d_(pm) the fast cycling pool of OC seemed completely exhausted at the end of the 91-days incubation
243 period.

244 The exponential Q_{10} model fitted the 91 days incubation data with an average R^2 of 0.97 (Fig. S1).
245 Logically, goodness of fit was slightly lower when based only on the date of the incubation period ($R^2=$
246 0.90; Fig. S2). In this last analysis, samples A2d_(PM), V4d_(PM), N2s_(AO) and V3d_(PO) which displayed
247 particularly low R^2 of 0.50, 0.65, 0.79, and 0.79, respectively; indicating an incompatibility between the
248 model and the data (i.e. See local decrease of mineralisation with increasing temperature in Fig. S2),
249 were thereafter excluded from the Q_{10} analysis. Mineralisation intensity estimated for the whole
250 incubation period, i.e. α , ranged from 0.3 to 5.0 mg.g⁻¹ with an average of 1.6 ± 1.4 mg.g⁻¹ (Fig. 2A), but
251 ranged between 0.1 and 0.6 mg.g⁻¹ with an average of 0.27 ± 0.15 mg.g⁻¹ when estimated from the last
252 step of the incubation period (Fig. 2B). Temperature sensitivity, i.e. Q_{10} , estimated at the end of the
253 incubation period ranged between 1.21 and 1.43 with an average of 1.28 ± 0.07 (Fig. 2C).
254 For the whole incubation period, α , significantly increased with depth within the 8 studied profiles
255 (paired T-test, $P=0.026$; Table 2, Fig. 2A and 3). When looking at the frost-regime effect, independently
256 from depth and profile considerations, mineralisation intensity was significantly higher in permafrost
257 than in active layers samples, i.e. 2.86 ± 1.58 and 0.90 ± 0.31 mg.g⁻¹, respectively (Mann-Whitney,
258 $P=0.005$; Table 2 and Fig. 2A). By contrast, mineralisation intensity was affected neither by site location
259 nor by organic vs. mineral soils (Table 2 and Fig. 2A). When estimated at the end of the incubation
260 period the mineralisation intensity was no longer affected by any investigated factors, i.e. site, soil type,
261 depth and permafrost (Table 2 and Fig. 2B). Similarly the Q_{10} estimated after the initial flush of
262 mineralisation after removal of the four samples with low R^2 was not affected by any investigated factors
263 (Table 2 and Fig. 2C).
264 The SOM composition varied mostly with sites and with the organic or mineral nature of the samples
265 whereas depth and frost regime did not have apparent effects, as indicated by sample distribution along
266 the two first axes of the correspondence analysis of the NMR data (Fig. 4). On the first axis (74% of
267 variability explained), Adventdalen stood apart from the other sites due to its higher proportion of Aryl C
268 and Ketonic/Aldehydic C and lower proportion of O-Alkyl C. On the second axis (20% of variability
269 explained), Neiden stood apart from Vorkuta due to a higher proportion of Carboxyl C and Alkyl C.
270 Mineral soils were relatively richer in Carboxyl C and Ketonic/Aldehydic C than organic ones. However,
271 no direct relationship could be found between SOM mineralisation parameters (i.e. Q_{10} and α) and the
272 NMR signature, even though linear, principal component and partial least square regressions were used.

273 With respect to the microbial community structure, the first two axes of the correspondence analysis
274 explained 68% of the variability for T-RFLP and only 47% for ARISA. As for SOM composition, the
275 analysis of bacterial and fungal community structures revealed significant differences among sites and
276 soil types but no effect of depth or frost regime (Fig. 5 and Fig. 6). According to an ANOVA performed
277 on the main CA axes, site effects explained at 40% ($p=0.001$) of the variability for fungi and 66%
278 ($p=0.001$) for bacteria, while soil type effects explained 23% ($p=0.001$) of the variability for fungi and
279 21% ($p=0.015$) for bacteria. The RDA performed on T-RFLP and ARISA showed that bacterial
280 communities were significantly structured by C/N ratio and aryl-C (Fig. S3), while fungal communities
281 were significantly structured by pH, OC, and aryl-C (Fig S4). The ANOVA performed on CA first axis of
282 T-RFLP and ARISA showed significant effect of bacterial community structure on Q_{10} only in interaction
283 with fungal community structure ($P<0.05$).

284

285 **4 Discussion**

286

287 **4.1 Mineralisation rate**

288 With mineralisation rates averaging $28 \pm 43 \mu\text{g C g}^{-1} \text{SOC d}^{-1}$, our data were in the lower range of values
289 recorded in similar permafrost affected soil studies. For instance, Wang et al. (2014) recorded values
290 ranging between 80-1280 $\mu\text{g C g}^{-1} \text{SOC d}^{-1}$ in an organic soil incubated between 5 and 25 °C, whereas
291 Dutta et al. (2006) recorded mineralization rates ranging between 235-1700 $\mu\text{g C g}^{-1} \text{SOC d}^{-1}$ in Siberian
292 mineral soils incubated between 5 and 15 °C. The temporal evolution of mineralisation rates that display
293 or not mineralisation flush of various intensity (Fig. 1) demonstrated that pools of different stability are
294 mineralized to different degrees in the different samples. Depth mainly but also presence of permafrost
295 (Table 2) had a clear effect on mineralisation rate, while, sampling site and soil types did not (Table 2). In
296 deep soil samples, strong mineralisation flushes indicated the presence of a substantial amount of fast
297 cycling carbon rapidly consumed at the beginning of the incubation, while the quasi absence of
298 mineralisation flush in shallow samples advocate for a reduced accumulation of fast cycling carbon in the
299 top of arctic soil profiles. Similarly, the incubation of the first 20 cm of a mountain permafrost profile did
300 not generate any mineralisation flushes Wang et al. (2014). This depth effect on the mineralisation rate
301 can be due to the conjugated action of a decreasing microbial activity with depth (Waldrop et al., 2010)

302 and a leaching/accumulation of fast cycling OC at depth due to the presence of permafrost. Arctic soil
303 can have labile carbon protected in deep permafrost, such as reported by Michaelson et al. (2004).
304 Finally, transient mineralization flush whose timing and intensity seem to be directly related to the
305 temperature, as observed for samples A2d(pm) and V3d(po), could be explained either by a temperature
306 dependant release of fast cycling OC such as through desorption and depolymerisation processes.

307

308 **4.2 Mineralisation intensity, α**

309 Mineralisation intensity estimated over the whole incubation period significantly increased with depth
310 and was significantly higher in permafrost than in active-layer samples (Table 2 and Fig. 2A). However,
311 when estimated for the last step of incubation, after the complete disappearance of the initials flushes of
312 mineralisation, no particular trend could be observed anymore (Table 2 and Fig. 2B), suggesting that the
313 higher mineralisation intensity observed in deep/permafrost samples was strongly linked to the presence
314 of a mineralisation flush. By comparison, the incubation study of three Siberian permafrost affected
315 profiles did show any consistent effect of depth on mineralisation rate (Rodionow et al., 2006).

316 In our analyses we acknowledge an apparent confounding factor between depth and permafrost which is
317 difficult to avoid, as permafrost is always located at depth within soil profiles. Determining whether it is
318 depth or permafrost that is at the origin of the accumulation of fast cycling OC is rather difficult. Indeed,
319 on the one hand, the increase of α with depth ranged between -0.05 and 0.38 for the two profiles without
320 permafrost, and between 0.39 and 4.36 (average: 1.60) for the six other profiles with permafrost (Fig. 3),
321 suggesting that the apparent depth effect results from the permafrost effect. On the other hand, initial
322 flushes of mineralisation were more significantly associated to deep sample ($p=0.001$) than to permafrost
323 sample ($p=0.035$).

324 The transient nature of the mineralization flushes suggests that the pool of fast cycling OM in our
325 deep/permafrost samples was negligible. This finding is also supported by our NMR observations, which
326 did not reveal any significant difference in OM quality with permafrost and depth. As a consequence, the
327 higher intensity of mineralisation observed in deep permafrost samples should not persist longer than the
328 quick depletion of the fast cycling pool of OC that followed the thawing. Similarly, studying a database
329 of long term incubation of permafrost affected profiles Schädel et al. (2005) estimated that fast cycling
330 OC did not represent more than 5% of all OC in both organic and mineral soils.

331 Our results suggest that the difference in mineralization intensity between active and permafrost layers is
332 actually quite small after the initial mineralization flush has passed. In the longer term, this difference is
333 likely to be negligible as compared to the massive increase in mineralization rate induced by permafrost
334 thawing, which induces the sudden release of OM previously physically protected in ice clogged
335 aggregates (Dioumaeva et al., 2002; Dutta et al., 2006; Michaelson and Ping, 2003; Mikan et al., 2002;
336 Rivkina et al., 2000; Waldrop et al., 2010; Wang et al., 2013).

337

338 **4.3 Temperature sensitivity, Q₁₀**

339 For the 12 remaining samples that were satisfactorily suited to the exponential model, Q₁₀ estimated for
340 the last step of incubation after complete exhaustion of the fast cycling pool of OC did not display any
341 significant depth, permafrost, soil type or site effects (Table 2), suggesting that temperature sensitivity of
342 permafrost affected soil is homogenous

343 In the literature, the effect of permafrost on SOM decomposition temperature sensitivity is still poorly
344 documented (Table 3). Rodionow et al. (2006) who performed a 30 days preincubation followed by
345 parallel short term incubation incubations at 5 and 15 °C did not observe any differences in Q₁₀ between
346 active and permafrost layers. On the contrary, Waldrop et al. (2010) measured significantly lower Q₁₀
347 values in deeper permafrost layers (average 2.7) than in shallow active layers (average 7.5), when using
348 an incubation method where a given set of samples was subjected to a temperature increase from -5 to +5
349 °C,. However, their incubation procedure crossed the freezing point, which is between -2° and 0°C for
350 soil water according to Dioumaeva et al. (2002), and therefore could not provide a real estimate of the
351 SOM temperature sensitivity. Using a similar procedure with a 0 °C to 10 °C temperature ramp, Wang et
352 al. (2013) obtained results opposite to those of Waldrop et al. (2010), with Q₁₀ averaging 5.0 and 29.2 in
353 the active and the permafrost layer respectively.

354 In the literature, a clear consensus on the depth effect on Q₁₀ of permafrost-affected soils still has to
355 emerge. Wang et al. (2013, 2014) did not record any depth effect whereas Song et al. (2014) observed a
356 clear increase of Q₁₀ with depth, which was independent from the depth of the transition from active to
357 permafrost layer. In non-arctic soils, Q₁₀ has been found either to remain constant (Reichstein et al.,

358 2005) or to increase with depth (Graf et al., 2008; Jin et al., 2008; Pavelka et al., 2007; Shi et al., 2006;
359 Tang et al., 2003; Wang et al., 2006; Xu and Qi, 2001).

360 Our synthesis of Q₁₀ values for permafrost-affected soils did not reveal any consistent soil type, depth or
361 permafrost effects (Table 3). This apparent absence of effect might be due to the scarcity of data and the
362 lack of standardisation of the Q₁₀ measurements among studies (Table 3). The present study conducted
363 with a consistent methodology for three different locations did not allow us to evidence any consistent
364 Q₁₀ response either. These negative results, combined with the lack of consensus in the literature,
365 suggest that either there is no effect or that the effect is small and would require large standardized
366 datasets for quantifying its magnitude. In both cases, the use of single temperature sensitivity parameters
367 in dynamic SOM model appears justifiable.

368

369 **4.3 Controls of soil chemical and microbial population compositions**

370 In the present study we were not able to draw a clear relationship between OC dynamics in permafrost
371 affected soils, on the one hand, and soil chemical composition as investigated by NMR and microbial
372 community structures as investigated by TRFLP and ARISA on the other hand. Indeed, mineralisation
373 intensity, α , calculated for the whole incubation period, significantly increased with depth and
374 permafrost, while α and Q₁₀ calculated after complete exhaustion of the fast cycling pool of OC did not
375 seem to be affected by any investigated factors, i.e. site, soil type, depth, and permafrost (See summary
376 Table 4). By contrast, SOM quality as investigated by NMR and the structure of the microbial
377 community as investigated by TRFLP for bacteria and ARISA for fungi proved affected by both site and
378 soil type. In addition microbial community structure was significantly linked to SOM quality, as
379 evidenced by RDA analyses performed on T-RFLP and ARISA fingerprints, which showed that bacteria
380 were affected by pH, C/N ratio and Aryl C and fungi by pH, C, and Aryl C (Fig. S3 and S4).

381 However, the fact that the intensity of mineralisation was significantly related to the intensity of the flush
382 of mineralisation suggests that SOM composition does control the intensity of mineralisation after
383 thawing. This suggests that NMR spectroscopy was not sensitive enough to detect small variations in
384 SOM composition induced by the presence of a small pool of fast cycling OC in the sample that produced
385 a large flush of mineralisation.

386 Although different soil types and different sites were characterised by different SOM quality and
387 different microbial community structures no significant difference was observed in OC dynamic,
388 indicating a high level of functional redundancy within the microbial community. A link was reported by
389 Waldrop et al. (2010), between microbial abundances and Q10 in permafrost affected soil, suggesting
390 that microbial abundances more than structure is a driver of SOM dynamics. Our results are consistent
391 with those obtained recently on boreal forest soils by Coucheney et al. (2013), who reported that SOM
392 quality influences soil microbial communities, but observed no link between the latter and the Q₁₀.

393

394 **4.4 Potential consequences for arctic soil warming**

395 Our results indicate that deep thawed permafrost layers would initially release more CO₂ than shallow
396 active layers. This difference appears to be driven by a small fast-cycling OC pool, which suggests that
397 higher mineralisation rates in deep / thawed permafrost layers would only be short lived and concern only
398 marginal CO₂ emission. Furthermore, our results suggest that, once the fast cycling pool of OM is
399 depleted, there will be no more intrinsic difference in SOM mineralization kinetics between permafrost
400 affected soil layers and non-affected ones, neither in terms of mineralization intensity nor in terms of
401 temperature sensitivity. This absence of intrinsic difference in SOM response does not exclude
402 differences in mineralization rates in the field, as deeper layers experience different environmental
403 conditions such as limited aeration. However, in our study, these conditions did not appear to have
404 modified the microbial community structure in a way that would affect its capacity to decompose SOM,
405 as the microbial community structure measured on the frozen samples could not be linked to the SOC
406 dynamics. Overall, we estimated the Q₁₀ of our permafrost affected soils to average 1.3, which will
407 translate into a substantial increase in CO₂ emission as temperature rises in active and permafrost layers,
408 and is somewhat a conservative estimate as compared to literature values. The absence of marked
409 difference between permafrost- and active-layer SOM in response to warming also suggests that: 1)
410 active layer SOM is a fairly good model for permafrost SOM, and 2) the use of a single temperature
411 sensitivity parameter in land surface models for SOM decomposition in permafrost-affected soils appears
412 justified.

413

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421

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562

Table

Table 1 Soil sample characteristics

Sample Id#	Coordinates	Depth	Sample Type*	pH _(H₂O)	C %	N %	C:N
<i>Svalbard (Norway)</i>							
A1s	N78° 12'05.5"	20-50	S/A/M	4.64	1.39	0.05	29
A1d	E15° 50'03.8"	105-173	D/P/M	4.46	1.76	0.06	30
A2s	N78° 11'09.2"	20-40	S/A/M	5.16	2.47	0.12	21
A2d	E15° 55'29.4"	70-106	D/P/M	4.78	2.14	0.08	28
<i>Finnmark (Norway)</i>							
N1s	N69° 41'05.3"	20-57	S/A/O	3.52	58.85	1.67	35
N1d	E29° 01'57.2"	57-151	D/P/O	4.17	54.37	1.88	29
N2s	N69° 41'06.9"	30-50	S/A/O	4.21	57.46	1.95	29
N2d	E29° 11'46.1"	100-115	D/A/O	4.32	43.90	1.56	28
<i>Vorkuta (Russia)</i>							
V1s	N67°35'23.4'', E064°10'00.4''	20-37	S/A/M	5.81	2.12	0.12	17
V1d		55-105	D/P/M	6.40	1.36	0.09	16
V2s	N67°35'20.9'', E064°09'39.8''	20-40	S/A/M	4.69	1.85	0.12	16
V2d		40-80	D/A/M	6.10	0.16	0.01	27
V3s	N67°30'06.4'', E064°22'54.3''	20-50	S/A/O	4.59	53.69	2.85	19
V3d		60-100	D/P/O	5.51	18.91	1.22	16
V4s	N67°20'35.4'', E063°55'46.4''	20-60	S/A/M	6.43	2.55	0.18	14
V4d		70-100	D/P/M	7.48	0.36	0.01	26

* Sample types: (S) shallow, (D) deep, (A) active layer, (P) permafrost layer, (M) mineral soil, (O) organic soil.

Table 2 Comparison of the intensity of mineralisation, a , and the temperature sensitivity, Q_{10} , per sites, depth, frost regime and soil types, as well as, per intensity of mineralization flush observed.

Factors (<i>statistical test</i>)	Significance level	Significant Differences between groups (<i>number of observation</i>)
<u><i>Parameter: a (whole incubation)</i></u>		
Site ^(e)	ns	-
Depth ^(b)	*	$S_{(n=8)} < D_{(n=8)}$
Frost regime ^(c)	**	$A_{(n=10)} < P_{(n=6)}$
Soil type ^(d)	ns	-
<u><i>Parameter: a (last incubation step)</i></u>		
Site ^(e)	ns	-
Depth ^(b)	ns	-
Frost regime ^(c)	ns	-
Soil type ^(c)	ns	-
<u><i>Parameter: Q_{10} (last incubation step)</i></u>		
Site ^(e)	ns	-
Depth ^(b)	ns	-
Frost regime ^(a)	ns	-
Soil type ^(a)	ns	-

Significant difference between groups were tested using: (a) T test (2 groups) and (b) Paired T test (2groups of paired samples). When normality and equal variances conditions were not reached significant differences were tested using non-parametric test: (c) Mann-Whitney Rank Sum Test (2group), (d) Wilcoxon signed rank test (2groups of paired samples) and (e) Kruskal-Wallis anova on rank (>3 groups). Data were organised by location: (A: Adventdalen, N: Neiden, V: Vorkuta), Depth: (S: Shallow, D: Deep), Frost regime: (A: Active layer, P: Permafrost layer) and soil type(M: Mineral, O: Organic), Mineralisation flush intensity (NF: low mineralization flush, F: high mineralization flush). Significance levels are marked as follow: ns ($P > 0.05$), * ($P < 0.05$); and ** ($P < 0.01$).

Table 3 Q₁₀ from incubation studies of Boreal, Arctic and Alpine permafrost affected soils.

Soil type	Permafrost sample	Incubation temperature (°C)	Q ₁₀ range	Reference	Q ₁₀ estimation methods
Mineral	yes	+5 to +15	1.7 - 2.9	Dutta et al., 2006	Long term (90 days) parallel incubation* (Q ₁₀ : derived from final cumulated data).
Mineral	no	+5 to +15	1.4 - 2.9	Rodionow et al., 2006	30 days preincubation at 5°C followed by parallel short term incubation*
Mineral	yes	+5 to +15	1.8 - 2.7	Rodionow et al., 2006	30 days preincubation at 5°C followed by parallel short term incubation*
Mineral	no	-5 to +5	6.8 - 9.0	Waldrop et al., 2010	Ramp of temperature†
Mineral	yes	-5 to +5	2.3 – 3.1	Waldrop et al., 2010	Ramp of temperature†
Organic	no	-5 to +5	6.6	Waldrop et al., 2010	Ramp of temperature†
Organic	yes	-5 to +5	2.7	Waldrop et al., 2010	Ramp of temperature†
Organic	no	-10 to +8	3.1 - 4.4	Dioumaeva et al., 2002	15 days preincubation at 4 °C, followed by parallel long term (60 days) incubation* (Q ₁₀ : derived from 5 sampling dates)
Organic	no	0 to +10	6.9 – 13.0	Song et al., 2014	Ramp of temperature†
Organic	yes	0 to +10	13.5-34.6	Song et al., 2014	Ramp of temperature†
Organic	no	+5 to +20	1.8 - 2.5	Wang et al., 2010	long term (40 days) parallel incubation* (Q ₁₀ : average of 7 sampling dates)
Organic	no	0 to +10	4.2 – 5.1	Wang et al., 2013	Ramp of temperature†
Organic	yes	0 to +10	29.2	Wang et al., 2013	Ramp of temperature†
Organic	no	+5 to +25	2.0 - 2.2	Wang et al., 2014	long term (35 days) parallel incubation* (Q ₁₀ : average of 9 sampling dates)
Organic	no	+10 to +20	0.7 - 1.9	Wickland and Neff 2008	Long term (57 days) parallel incubation* (Q ₁₀ : derived from final cumulated data)

*Parallel incubation: Several samples incubated in parallel at different temperature.

†Ramp of temperature: The samples are submitted to increasing temperature.

Table 4: Summary of the observed significant effects

	Site effect	Soil type effect	Depth effect	permafrost effect
Mineralisation flush	No	No	Yes***	Yes*
α (whole incubation)	No	No	Yes*	Yes**
α (last step of incubation)	No	No	No	No
Q ₁₀	No	No	No	No
NMR (SOM quality)	Yes**	Yes**	No	No
TRFLP (Bacteria)	Yes***	Yes *	No	No
ARISA (Fungi)	Yes***	Yes***	No	No

Significant effects are notified by "Yes". Significance levels are marked by asterisk such as: * ($P < 0.05$); ** ($P < 0.01$); and *** ($P < 0.001$). For the CCA the level of significance was estimated by performing ANOVAs on the main axis. Absence of significance notified by "No". Significant effect in grey may indirectly results from another significant effect.

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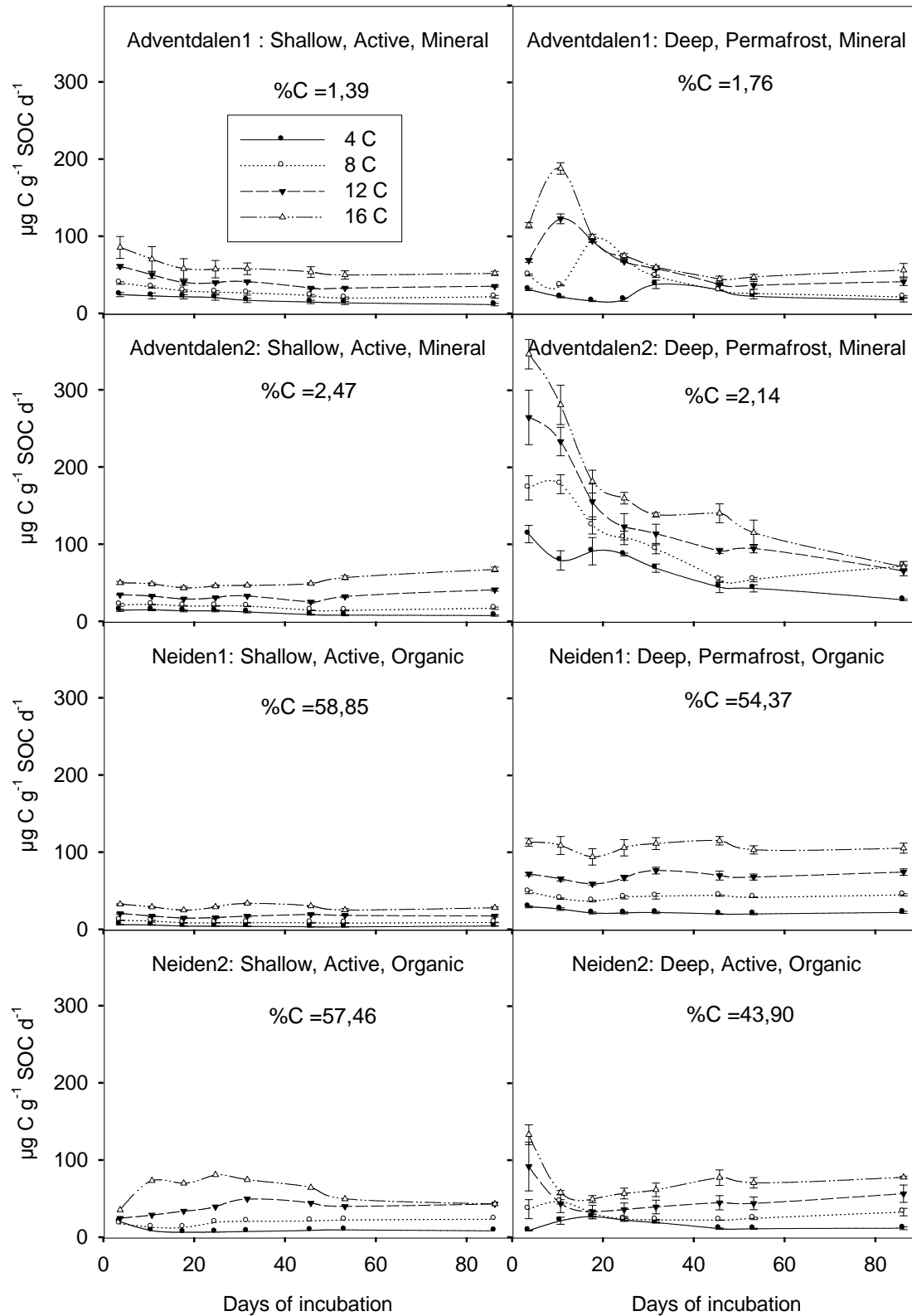


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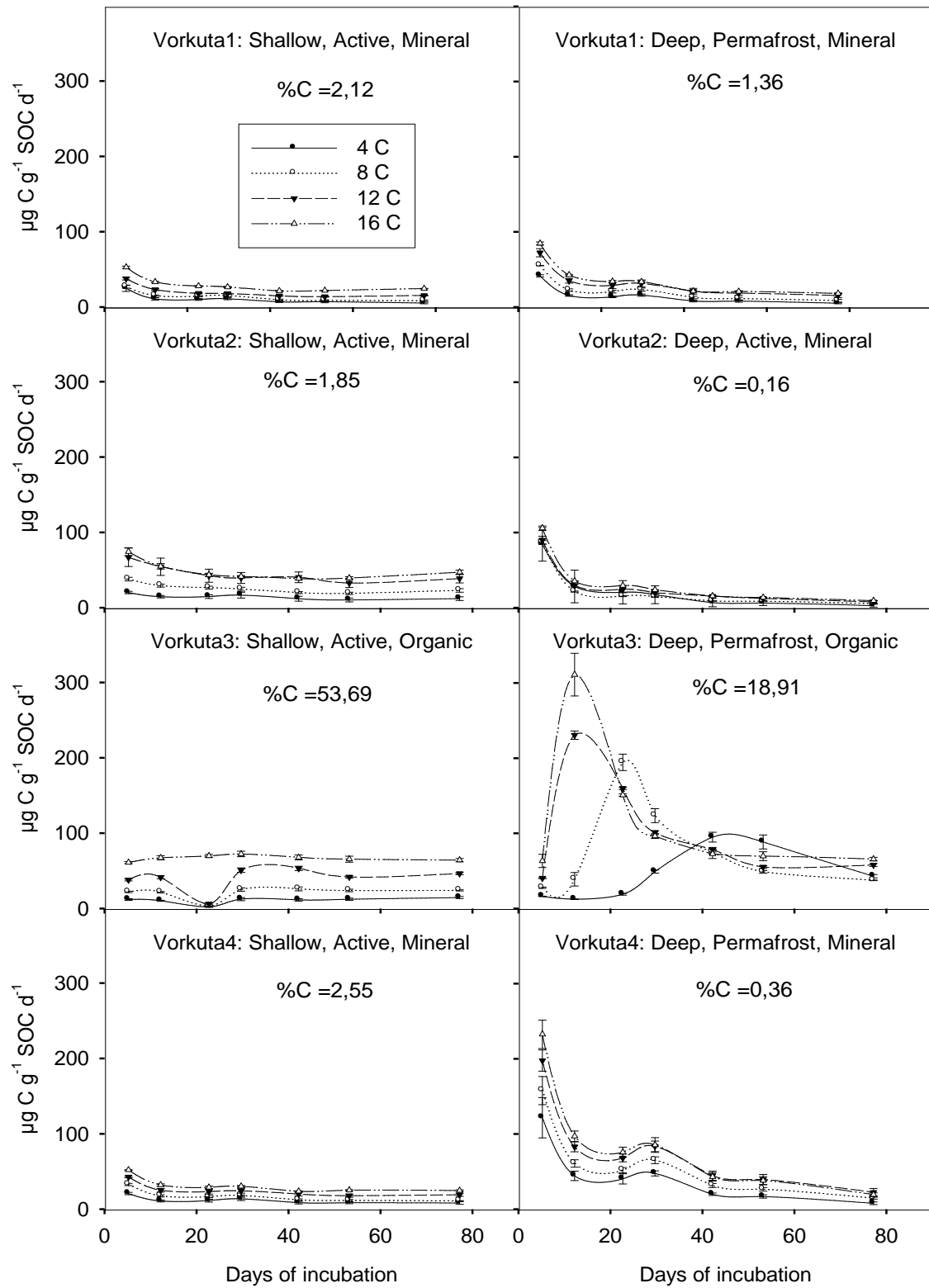


Fig. 1 bis Carbon fluxes rates through time over a 91 days incubation experiment at three constant temperatures (mean \pm SD).

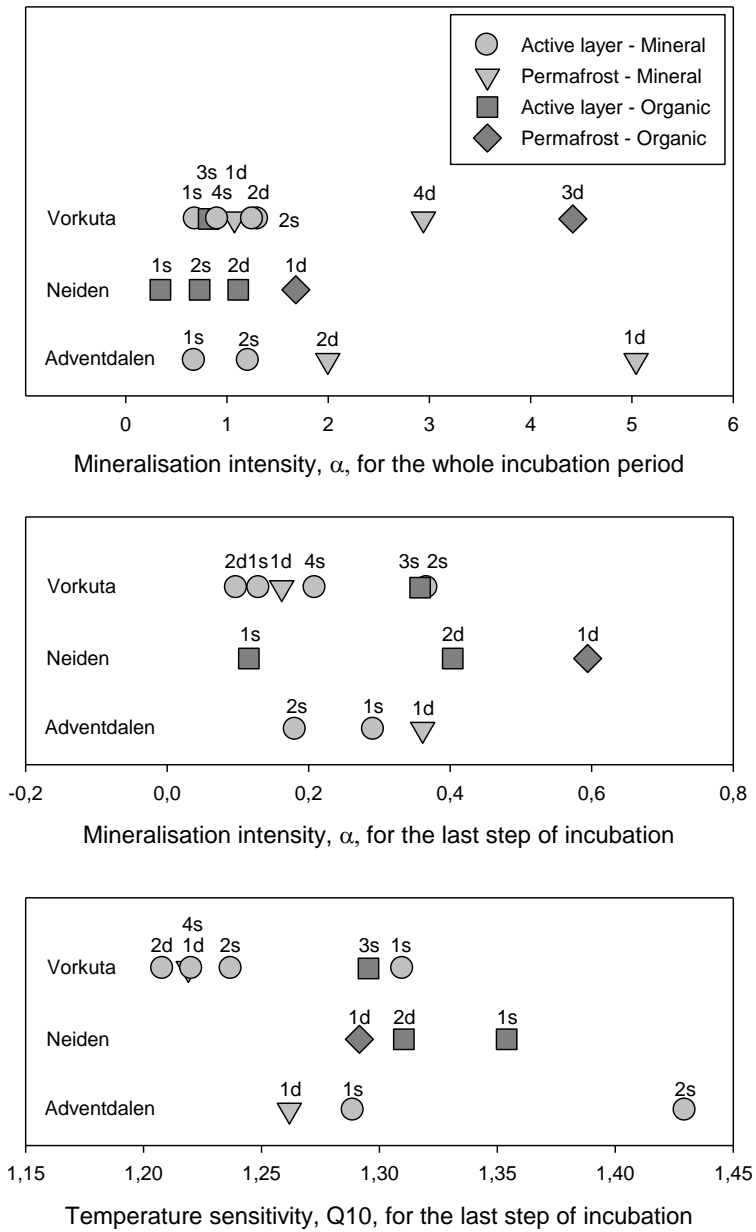


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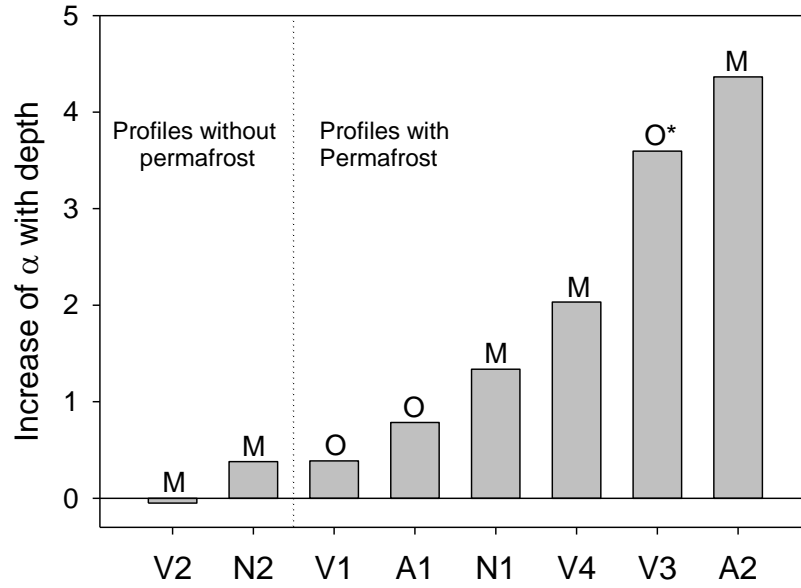


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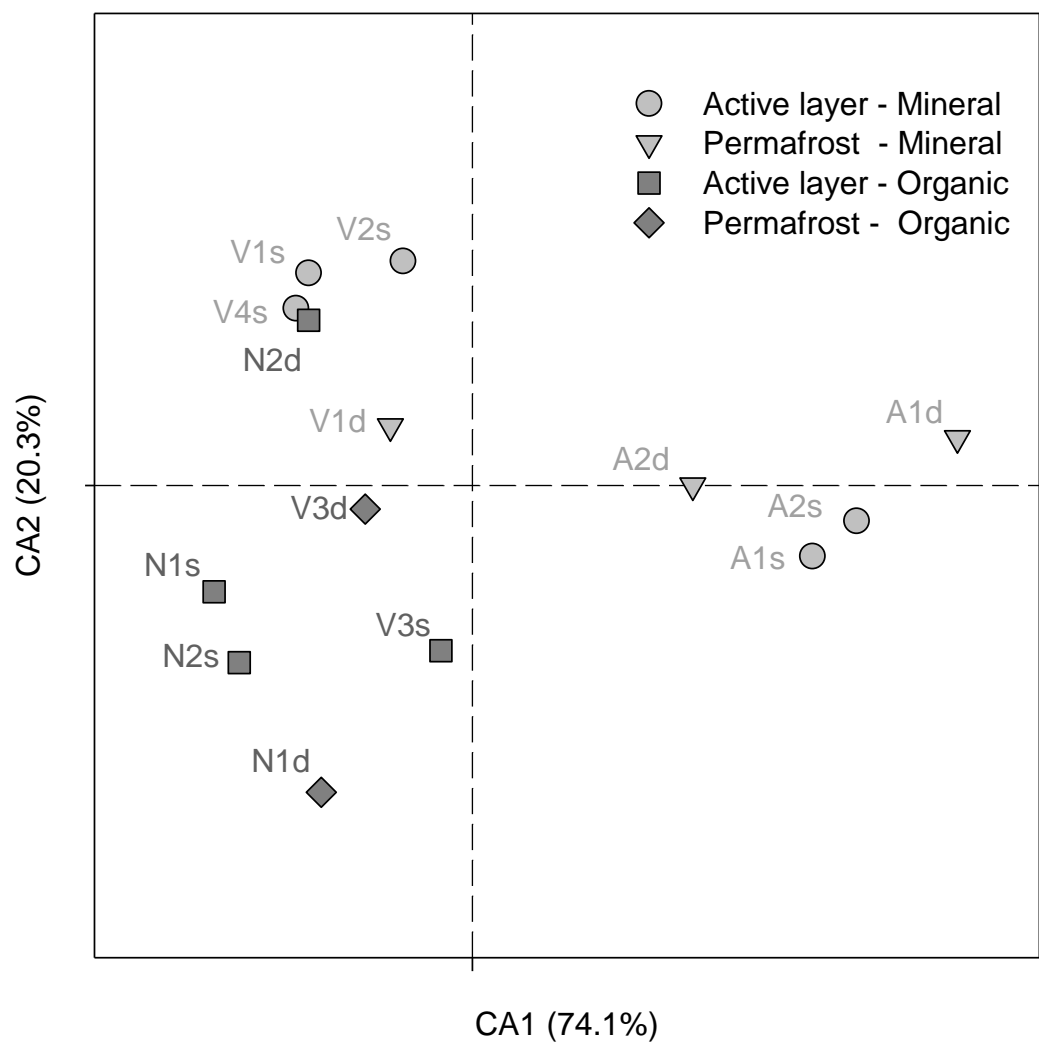


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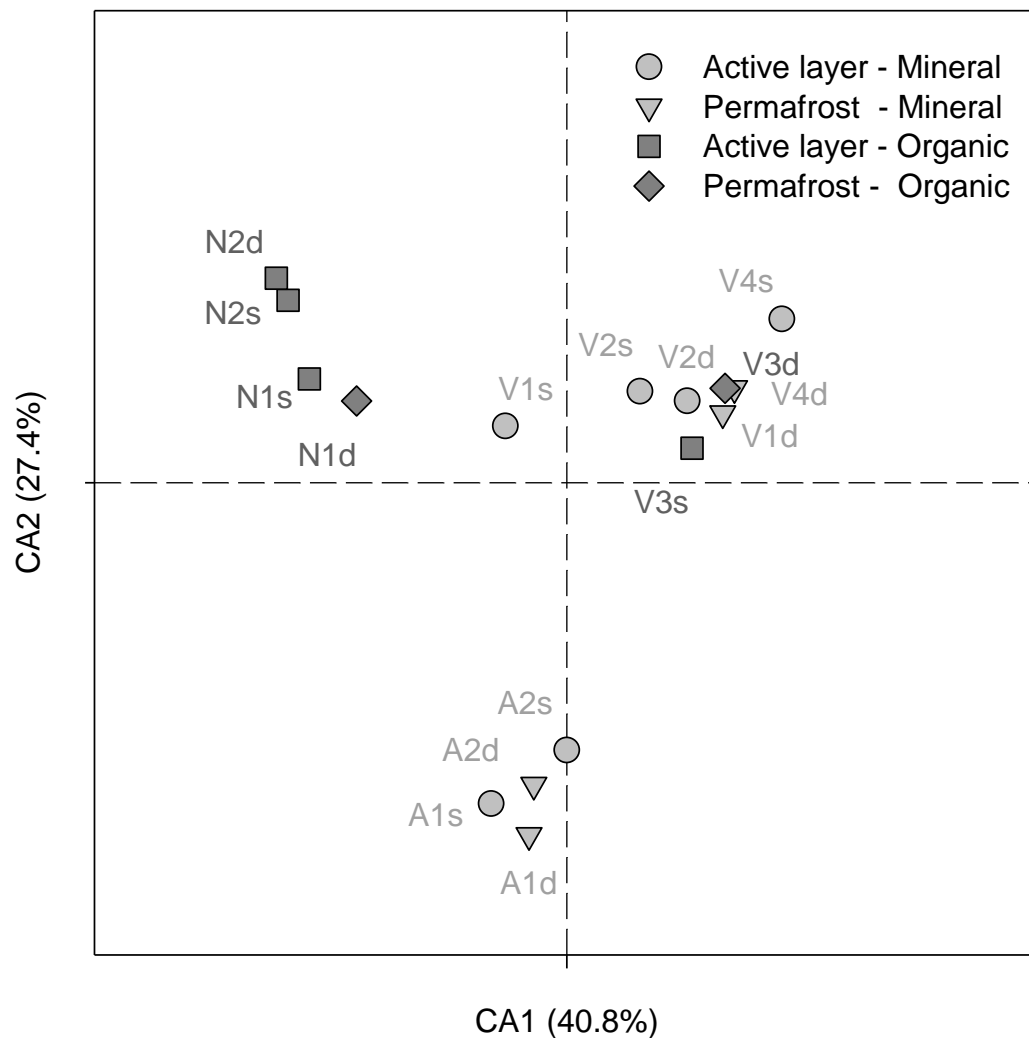


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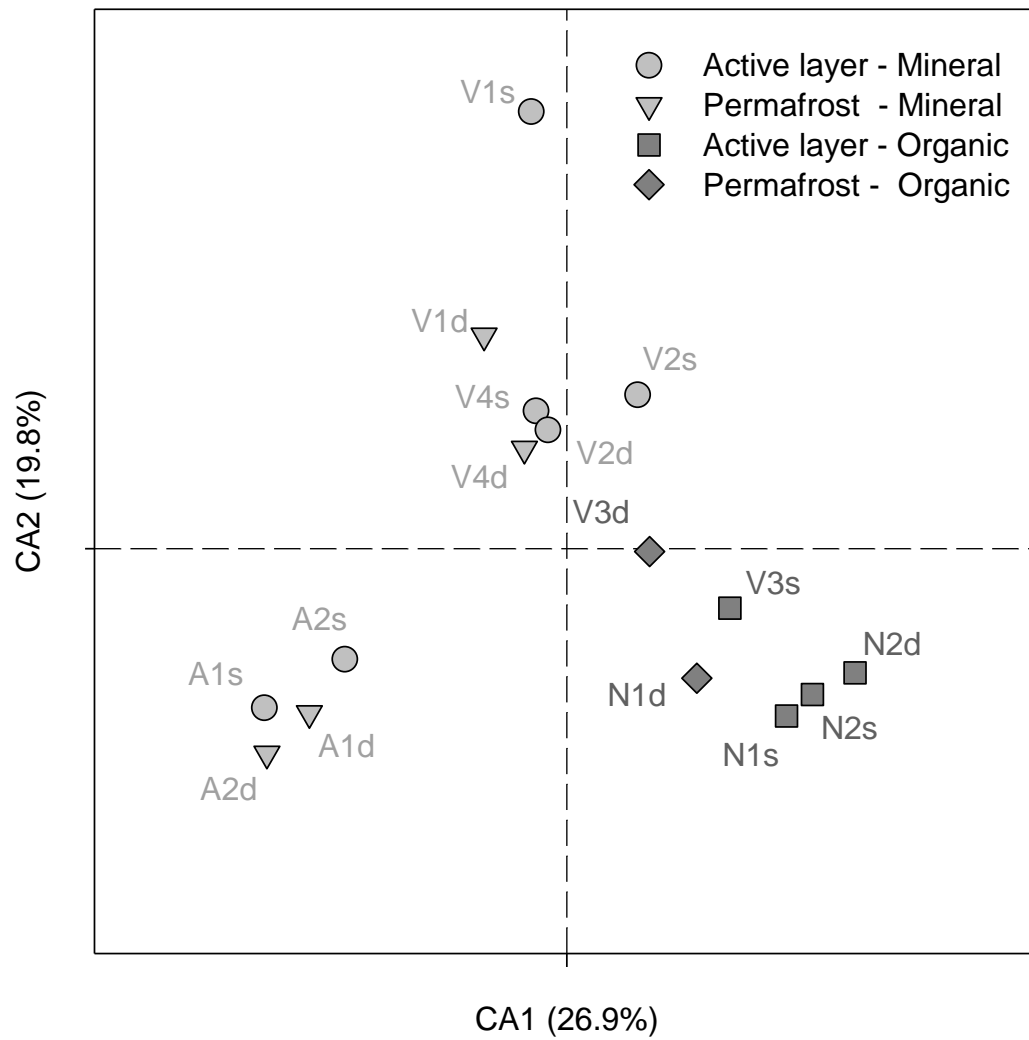


Fig. 6: Correspondence Analysis (46.7% of variability) performed on ARISA (Fungi) profiles expressed in percentage of relative amount of each fragment. Data used are the means of 3 replicates.

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