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Temperature response of soil organic matter mineralisation in arctic soil profiles

Questa è la Versione finale referata (Post print/Accepted manuscript) della seguente pubblicazione:

Original Citation:

Temperature response of soil organic matter mineralisation in arctic soil profiles / Moni, Christophe; Lerch, Thomas Z.; Knoth de Zarruk, Katrin; Strand, Line Tau; Forte, Claudia; Certini, Giacomo; Rasse, Daniel P.. - In: SOIL BIOLOGY & BIOCHEMISTRY. - ISSN 0038-0717. - STAMPA. - 88:(2015), pp. 236-246. [10.1016/j.soilbio.2015.05.024]

Availability:

This version is available at: 2158/1006459 since: 2021-03-30T19:14:02Z

Published version:

DOI: 10.1016/j.soilbio.2015.05.024

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02 February 2025

Elsevier Editorial System(tm) for Soil Biology and Biochemistry
Manuscript Draft

Manuscript Number: SBB9781R2

Title: Temperature response of soil organic matter mineralisation in arctic soil profiles

Article Type: Research Paper

Keywords: arctic peat soil; permafrost; mineralisation; temperature sensitivity; soil organic matter; soil microbial communities

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Manuscript Region of Origin: NORWAY

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

***Revision Notes**

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 expended 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 formated. A new reference list was generated using the same template and we hope that everything is in order now.

***Highlights (for review)**

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

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Temperature response of soil organic matter mineralisation in arctic soil profiles

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

Abstract

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 CO_2. 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 ^{13}C-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 where 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.

1 Introduction

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

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

2 Material and methods

2.1 Soil sampling and physico-chemical characterisation

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

2.2 Carbon mineralisation measurement

Moist samples at field capacity of mineral and organic soil, 50 and 20 g respectively, were incubated in triplicates in 250-ml serum vials. Prior to capping with CO_2-tight butyl-rubber stoppers, vials were flushed with compressed air. Thorough flushing of the vials containing the soil samples was controlled with an infra-red gas analyser (IRGA) (EGM-4 PP System, Amesbury, MA, USA). Flushing time of one minute proved to be sufficient to reach the CO_2 concentration of compressed air, i.e. 147 ± 2 ppm. Butyl-rubber stoppers were partially inserted before removing the flushing tube, so that end of flushing and capping were simultaneous. Serum vials were placed in triplicates in incubators in the dark for 91 days at 4, 8, 12, and 16 °C. Moisture content was kept constant during the course of the entire incubation period by weighing each sample and spraying distilled water to compensate for any water loss. Measurements of soil C mineralisation were performed at approximately two-week intervals over a 91-day period. Carbon mineralisation rates were determined by measuring the accumulated CO_2 concentration in the vial headspace. Measurements were performed with a micro gas chromatograph (Agilent 3000 Micro-GC, France). Samples were flushed and recapped at intervals that prevented the headspace CO_2 concentration to ever exceed 35000 ppm, the value at which anaerobic thresholds have been reported (MacFadye, 1973). Samples were capped between 4 and 14 days before measurements.

2.3 Analysis of soil organic matter by ^{13}C-CPMAS NMR

Solid-state ^{13}C-CPMAS NMR spectra were recorded on a Bruker AMX 300-WB spectrometer equipped with a 4 mm CPMAS probe. Experimental conditions were: 90^{o} pulse = 3.1 µs, contact time = 3 ms, relaxation delay = 3s, spinning rate = 8 kHz, and number of scans between 8,000 and 32,000 depending on the SOM content of the sample. The soil samples were indirectly enriched in C selectively removing single sand grains by hand-picking under a 20x lens. Then they were treated with 2% hydrofluoric acid as in Skjemstad et al. (1994) to remove paramagnetic materials, which give rise to broadened resonances and signal loss. The combined mechanical and chemical treatments for preparing soil samples for the NMR analysis increased the C concentration in the Adventdalen and Vorkuta samples by 80 to 220%, which allowed high quality spectra to be obtained, except for the non-frozen deep layer of $V2_{(AM)}$, which, despite the treatments, had a too low C content. A semi-quantitative estimation of the main C forms was obtained by integrating five chemical shift regions (0-45 ppm, alkyl C; 45-110 ppm, O-alkyl C; 110-165 ppm, aryl C; 165-185 ppm, carboxyl C; 185-220 ppm, carbonyl C) and expressing them as percentages of the total spectral intensity; where observed, the contribution of rotational sidebands, often observed for aryl and carbonyl/carboxyl resonances, was taken into account (Smernik et al., 2008)

2.4 Microbial communities profiling

Bacterial and fungal communities were analysed using a Terminal restriction fragment length polymorphism (T-RFLP; Osborn et al., 2000) and automated ribosomal intergenic spacer analysis (ARISA; Ranjard et al., 2003), respectively. The DNA was extracted from 0.25 g of soil using the FastDNA™ SPIN Kit for Soil (MP Biomedicals) according to the manufacturer's instructions. Bacterial 16S rRNA gene was amplified using primers 63F (5'-CAGGCCTAACACATGCAAGTC-3') fluorescently labelled at the 5' end with FAM dye and 1389R (5'-ACGGGCGGTGTGTACAAG-3') (Marchesi et al., 1998). Fungal internal transcribed spacers (ITS) were amplified, using the primers ITS1F (5'-CTTGGTCATTTAGAGGAAGTAA-3') (Gardes and Bruns, 1993) fluorescently labelled at the 5' end with Yakima Yellow® dye and ITS4 (5'-TCCTCCGCTTATTGATATGC). PCR were performed with 2µL of diluted (1:10) DNA template in a total volume of 20µL (Master Mix Kit, Qiagen) and 0.05 mM of each primer. Biorad T100 thermal cycler was used for the amplification with the following programmes for T-RFLP: initial denaturation at 94 ºC for 2 min, followed by 30 cycles of 94 ºC for 30 s, 57 ºC for 45 s, and 72 ºC for 90 s, followed by a final extension time at 72 ºC for 10 min. For ARISA, PCR conditions consisted of an initial denaturation at 95 ºC for 5 min, followed by 35 cycles of 95 ºC for 30 s, 55 ºC for 30 s, and 72 ºC for 60 s, followed by a final extension time at 72 ºC for 10. Bacterial PCR products (10 µl) were digested with 10 U of the restriction enzyme AluI and 1× restriction enzyme buffer (Thermo Fisher) in a total volume of 15 µl at 37 ºC for 3 h. After a desalting step, 2µl of PCR products were mixed with formamide containing 0.5% of ROX-labelled GS500 (T-RFLP) or GS2500 (ARISA) internal size standard (Applied Biosystems,) in a total volume of 12 µl and denatured at 94 ºC for 3 min. Samples were electrophoresed on an ABI 3730 PRISM® capillary DNA sequencer (Applied Biosystems). The T-RFLP and ARISA profiles obtained with the sequencer were analysed using GeneMapper® v3.7 software (Applied Biosystems). The fragments between 50 and 500 bp and peaks height ≥ 50 fluorescence units were included inT-RFLP analysis and Amplicons between 200 and 1500 bp and peaks height ≥ 100 fluorescence units were included for ARISA analysis. Fragments having a relative abundance of proportion < 0.5% were removed from the matrices.

2.5 Temperature sensitivity

2.5.1 Choice of method

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

2.5.2 Calculation

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

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

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

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

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

2.7 Statistical analysis

All mineralisation curves were fitted using nonlinear procedures allowing for weighting (nls function) of the R software (R 2.13.1©2011 The R foundation for statistical computing). Data point weight was inversely proportional to SD. Parameters of SOM temperature sensitivity responses were analysed as a function of sample location, depth, frost regime and soil type. Significant difference between groups were tested using: (a) T test (two groups), (b) Paired T test (two groups of paired samples) and (c) ANOVA (> two groups). When normality and equal variances conditions were not reached significant differences were tested using non-parametric test: (d) Mann-Whitney Rank Sum Test (two groups), (e) Wilcoxon signed rank test (two groups of paired samples), and (f) Kruskal-Wallis ANOVA on rank (> two groups). Dunn or Holm-Sidak multiple comparison tests (with 95% confidence limits) were further used to test for differences between sample categories. Fisher exact test was used to identify significant association within contingency tables. Tests a, b, c, d, e, f and Fisher exact test were performed using the SigmaPlot software (SigmaPlot 11.0 © 2008 Systat Software, Inc.). SOM composition and microbial communities structure of each sample were compared by correspondence analysis (CA) using the proportion of NMR functional groups (Alkyl C, O-alkyl C, Aryl C, Carboxyl C, Ketonic/Aldehydic C) and the relative abundance of genetic fragments (TRFLP and ARISA matrices), respectively. Redundancy analyses (RDA) were further performed to explore the relationships between microbial communities and soil chemical properties. All multivariate analyses were performed using the "ade4TkGUI" package in R while graphic representations were performed with SigmaPlot 11.0.

3 Results

The measured pH values of the investigated soils were all (except in $V4d_{(PM)}$) below neutrality (Table 1), which leads to exclude the presence of carbonates and, as a consequence, their contribution to CO_2 emission during the incubation measurements (Tamir et al., 2011; Ramnarine et al., 2012). Mineralisation rate ranged between 0.05 and 387.34 µg C g^{-1} SOC d^{-1} and averaged 28 ± 43 µg C g^{-1} SOC d^{-1} (Fig. 1) At the end of the 91-day incubation period the proportion of mineralised OC averaged 2.2 ± 1.5; 3.6 ± 2.5; 5.4 ± 3.2 and 7.1 ± 4.1 mg.g^{-1} at 4, 8, 12, and 16 ^{o}C, respectively (Fig. S1). For all soil profiles but $V2_{(AM)}$, the proportion of mineralised OC at the end of the incubation period was significantly higher in the deep soil samples than in the shallow ones. Considering permafrost-affected profiles only, the proportion of mineralised OC was always significantly higher in the deep permafrost layer than in the shallow active layer. Instantaneous mineralisation rate recorded over the 91-day incubation period (Fig. 1) clearly showed that SOM of increasing stability is mineralized during the incubation period. Three different patterns were observed. While some samples experienced a strong initial mineralisation flush at the beginning of the incubation period followed by a strong decline of the mineralisation rate (i.e $A2d_{(PM)}$, $N2d_{(AO)}$, $V1d_{(PM)}$, $V2d_{(AM)}$, $V4d_{(Pm)}$), others displayed rather stable mineralisation rate in time with no, or, almost no, initial mineralisation flush (i.e. $A1s_{(AM)}$, $A2s_{(AM)}$, $N1s_{(AO)}$, $N1d_{(PO)}$, $N2s_{(AO)}$, $V3s_{(AO)}$, $V1s_{(AM)}$, $V2s_{(AM)}$, $V4s_{(AM)}$). Finally two samples, $A1d_{(pm)}$ and $V3d_{(po)}$, presented a strong and sharp transient increase of mineralisation rate that declined faster at higher temperatures with faster depletion of substrates. Fisher exact test, showed that strong mineralisation flushes, initial or delayed, were significantly associated to deep samples (p = 0.001) and to a lesser extent to permafrost samples (p = 0.035), while the distribution of the strong and weak mineralisation flush within soil types (i.e organic vs. mineral) did not diverge significantly from a random distribution. For all soils, with maybe the exception of $A2d_{(pm)}$ the fast cycling pool of OC seemed completely exhausted at the end of the 91-days incubation period.

The exponential Q_{10} model fitted the 91 days incubation data with an average R^2 of 0.97 (Fig. S1). Logically, goodness of fit was slightly lower when based only on the date of the incubation period (R^2= 0.90; Fig. S2). In this last analysis, samples $A2d_{(PM)}$, $V4d_{(PM)}$, $N2s_{(AO)}$ and $V3d_{(PO)}$ which displayed particularly low R^2 of 0.50, 0.65, 0.79, and 0.79, respectively; indicating an incompatibility between the model and the data (i.e. See local decrease of mineralisation with increasing temperature in Fig. S2), were thereafter excluded from the Q_{10} analysis. Mineralisation intensity estimated for the whole 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 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 step of the incubation period (Fig. 2B). Temperature sensitivity, i.e. Q_{10}, estimated at the end of the incubation period ranged between 1.21 and 1.43 with an average of 1.28 ± 0.07 (Fig. 2C).

For the whole incubation period, α, significantly increased with depth within the 8 studied profiles (paired T-test, *P*=0.026; Table 2, Fig. 2A and 3). When looking at the frost-regime effect, independently from depth and profile considerations, mineralisation intensity was significantly higher in permafrost than in active layers samples, i.e. 2.86 ± 1.58 and 0.90 ± 0.31 $mg.g^{-1}$, respectively (Mann-Whitney, P=0.005; Table 2 and Fig. 2A). By contrast, mineralisation intensity was affected neither by site location nor by organic vs. mineral soils (Table 2 and Fig. 2A). When estimated at the end of the incubation period the mineralisation intensity was no longer affected by any investigated factors, i.e. site, soil type, depth and permafrost (Table 2 and Fig. 2B). Similarly the Q_{10} estimated after the initial flush of mineralisation after removal of the four samples with low R^2 was not affected by any investigated factors (Table 2 and Fig. 2C).

The SOM composition varied mostly with sites and with the organic or mineral nature of the samples whereas depth and frost regime did not have apparent effects, as indicated by sample distribution along the two first axes of the correspondence analysis of the NMR data (Fig. 4). On the first axis (74% of variability explained), Adventdalen stood apart from the other sites due to its higher proportion of Aryl C and Ketonic/Aldehydic C and lower proportion of O-Alkyl C. On the second axis (20% of variability explained), Neiden stood apart from Vorkuta due to a higher proportion of Carboxyl C and Alkyl C. Mineral soils were relatively richer in Carboxyl C and Ketonic/Aldehydic C than organic ones. However, no direct relationship could be found between SOM mineralisation parameters (i.e. Q_{10} and α**)** and the NMR signature, even though linear, principal component and partial least square regressions were used.

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

4 Discussion

4.1 Mineralisation rate

With mineralisation rates averaging 28 ± 43 µg C g^{-1} SOC d^{-1}, our data were in the lower range of values recorded in similar permafrost affected soil studies. For instance, Wang et al. (2014) recorded values ranging between 80-1280 µg C g^{-1} SOC d^{-1} in an organic soil incubated between 5 and 25 ^{o}C, whereas Dutta et al. (2006) recorded mineralization rates ranging between 235-1700 µg C g^{-1} SOC d^{-1} in Siberian mineral soils incubated between 5 and 15 ^{o}C. The temporal evolution of mineralisation rates that display or not mineralisation flush of various intensity (Fig. 1) demonstrated that pools of different stability are mineralized to different degrees in the different samples. Depth mainly but also presence of permafrost (Table 2) had a clear effect on mineralisation rate, while, sampling site and soil types did not (Table 2). In deep soil samples, strong mineralisation flushes indicated the presence of a substantial amount of fast cycling carbon rapidly consumed at the beginning of the incubation, while the quasi absence of mineralisation flush in shallow samples advocate for a reduced accumulation of fast cycling carbon in the top of arctic soil profiles. Similarly, the incubation of the first 20 cm of a mountain permafrost profile did not generate any mineralisation flushes Wang et al. (2014). This depth effect on the mineralisation rate can be due to the conjugated action of a decreasing microbial activity with depth (Waldrop et al., 2010) and a leaching/accumulation of fast cycling OC at depth due to the presence of permafrost. Arctic soil can have labile carbon protected in deep permafrost, such as reported by Michaelson et al. (2004).

Finally, transient mineralization flush whose timing and intensity seem to be directly related to the temperature, as observed for samples A2d(pm) and V3d(po), could be explained either by a temperature dependant release of fast cycling OC such as through desorption and depolymerisation processes.

4.2 Mineralisation intensity, *α*

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

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

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

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

4.3 Temperature sensitivity, Q10

For the 12 remaining samples that were satisfactorily suited to the exponential model, Q_{10} estimated for the last step of incubation after complete exhaustion of the fast cycling pool of OC did not display any significant depth, permafrost, soil type or site effects (Table 2), suggesting that temperature sensitivity of permafrost affected soil is homogenous

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

In the literature, a clear consensus on the depth effect on Q10 of permafrost-affected soils still has to emerge. Wang et al. (2013, 2014) did not record any depth effect whereas Song et al. (2014) observed a clear increase of Q10 with depth, which was independent from the depth of the transition from active to permafrost layer. In non-arctic soils, Q_{10} has been found either to remain constant (Reichstein et al.,

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

Our synthesis of Q10 values for permafrost-affected soils did not reveal any consistent soil type, depth or permafrost effects (Table 3). This apparent absence of effect might be due to the scarcity of data and the lack of standardisation of the Q_{10} measurements among studies (Table 3). The present study conducted with a consistent methodology for three different locations did not allow us to evidence any consistent Q10 response either. These negative results, combined with the lack of consensus in the literature, suggest that either there is no effect or that the effect is small and would require large standardized datasets for quantifying its magnitude. In both cases, the use of single temperature sensitivity parameters in dynamic SOM model appears justifiable.

4.3 Controls of soil chemical and microbial population compositions

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

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

Although different soil types and different sites were characterised by different SOM quality and different microbial community structures no significant difference was observed in OC dynamic, indicating a high level of functional redundancy within the microbial community. A link was reported by Waldrop et al. (2010), between microbial abundances and Q10 in permafrost affected soil, suggesting that microbial abundances more than structure is a driver of SOM dynamics. Our results are consistent with those obtained recently on boreal forest soils by Coucheney et al. (2013), who reported that SOM quality influences soil microbial communities, but observed no link between the latter and the Q_{10}.

4.4 Potential consequences for arctic soil warming

Our results indicate that deep thawed permafrost layers would initially release more CO_2 than shallow active layers. This difference appears to be driven by a small fast-cycling OC pool, which suggests that higher mineralisation rates in deep / thawed permafrost layers would only be short lived and concern only marginal CO_2 emission. Furthermore, our results suggest that, once the fast cycling pool of OM is depleted, there will be no more intrinsic difference in SOM mineralization kinetics between permafrost affected soil layers and non-affected ones, neither in terms of mineralization intensity nor in terms of temperature sensitivity. This absence of intrinsic difference in SOM response does not exclude differences in mineralization rates in the field, as deeper layers experience different environmental conditions such as limited aeration. However, in our study, these conditions did not appear to have modified the microbial community structure in a way that would affect its capacity to decompose SOM, as the microbial community structure measured on the frozen samples could not be linked to the SOC dynamics. Overall, we estimated the Q10 of our permafrost affected soils to average 1.3, which will translate into a substantial increase in CO_2 emission as temperature rises in active and permafrost layers, and is somewhat a conservative estimate as compared to literature values. The absence of marked difference between permafrost- and active-layer SOM in response to warming also suggests that: 1) active layer SOM is a fairly good model for permafrost SOM, and 2) the use of a single temperature sensitivity parameter in land surface models for SOM decomposition in permafrost-affected soils appears justified.

Acknowledgments

The present research was financially supported by the Research Council of Norway, NORKLIMA programme, project PERMASOM 184754/S30. Galina Mazhitova, Monica Votvik, Alexander Pastukhov, Paul Erik Aspholm, Tore Sveistrup, Hanne Christiansen are gratefully acknowledged for helping with soil sample collection. The authors wish to thank Caroline Roelandt and Annelene Pengerud for useful comments on an earlier version of this manuscript and Battle Karimi for advices on statistical analysis.

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Table

Table

Table 1 Soil sample characteristics

Sample Id#	Coordinates	Depth	Sample Type*	$pH_{(H2O)}$	C %	N %	C:N
Svalbard (Norway)							
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
Finnmark (Norway)							
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
Vorkuta (Russia)							
V1s	N67°35'23.4'',	20-37	S/A/M	5.81	2.12	0.12	17
V1d	E064°10'00.4''	55-105	D/P/M	6.40	1.36	0.09	16
V2s	N67°35'20.9'',	20-40	S/A/M	4.69	1.85	0.12	16
V2d	E064°09'39.8''	40-80	D/A/M	6.10	0.16	0.01	27
V3s	N67°30'06.4'',	20-50	S/A/O	4.59	53.69	2.85	19
V3d	E064°22'54.3''	60-100	D/P/O	5.51	18.91	1.22	16
V4s	N67°20'35.4'',	20-60	S/A/M	6.43	2.55	0.18	14
V4d	E063°55'46.4''	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, <u>*a*</u>, and the temperature sensitivity, Q_{10}, per sites, depth, frost regime and soil types, as well as, per intensity of mineralization flush observed.

Factors *(statistical test)*	Significance level	Significant Differences between groups *(number of observation)*
<u>*Parameter: a (whole incubation)*</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>*Parameter: a (last incubation step)*</u>		
Site[e]	ns	-
Depth[b]	ns	-
Frost regime[c]	ns	-
Soil type[c]	ns	-
<u>*Parameter: Q_{10} (last incubation step)*</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 Q_{10} 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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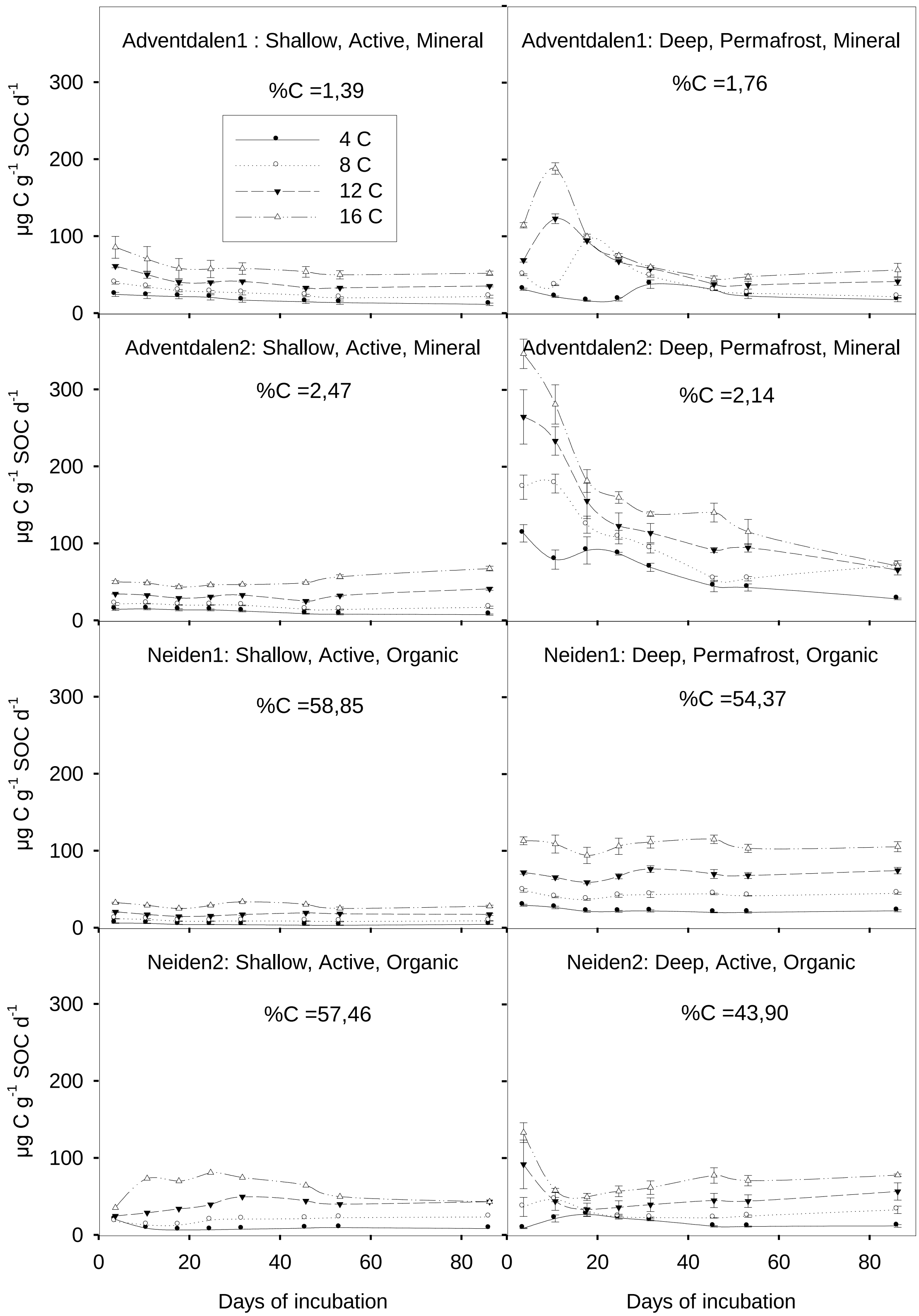

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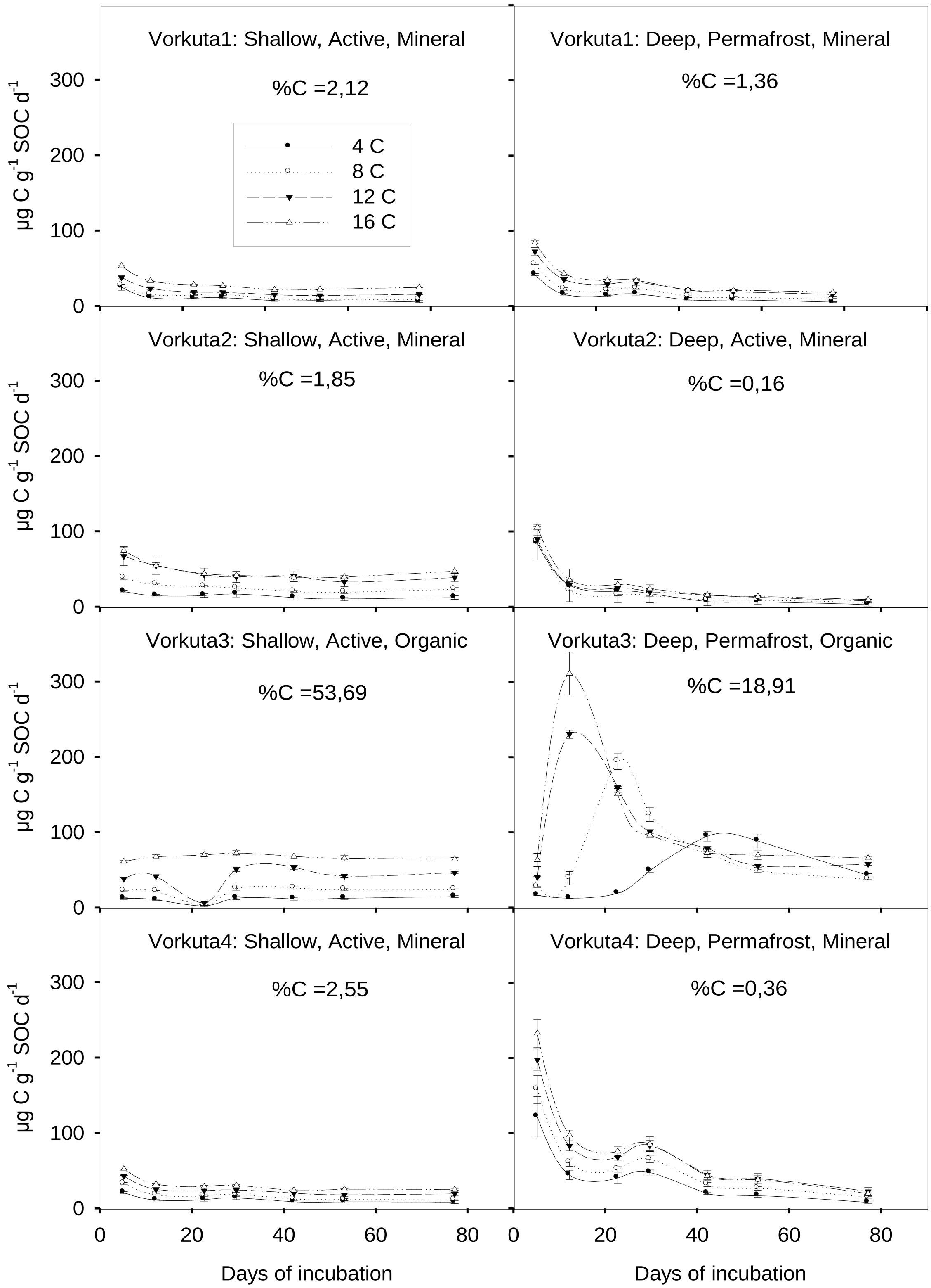

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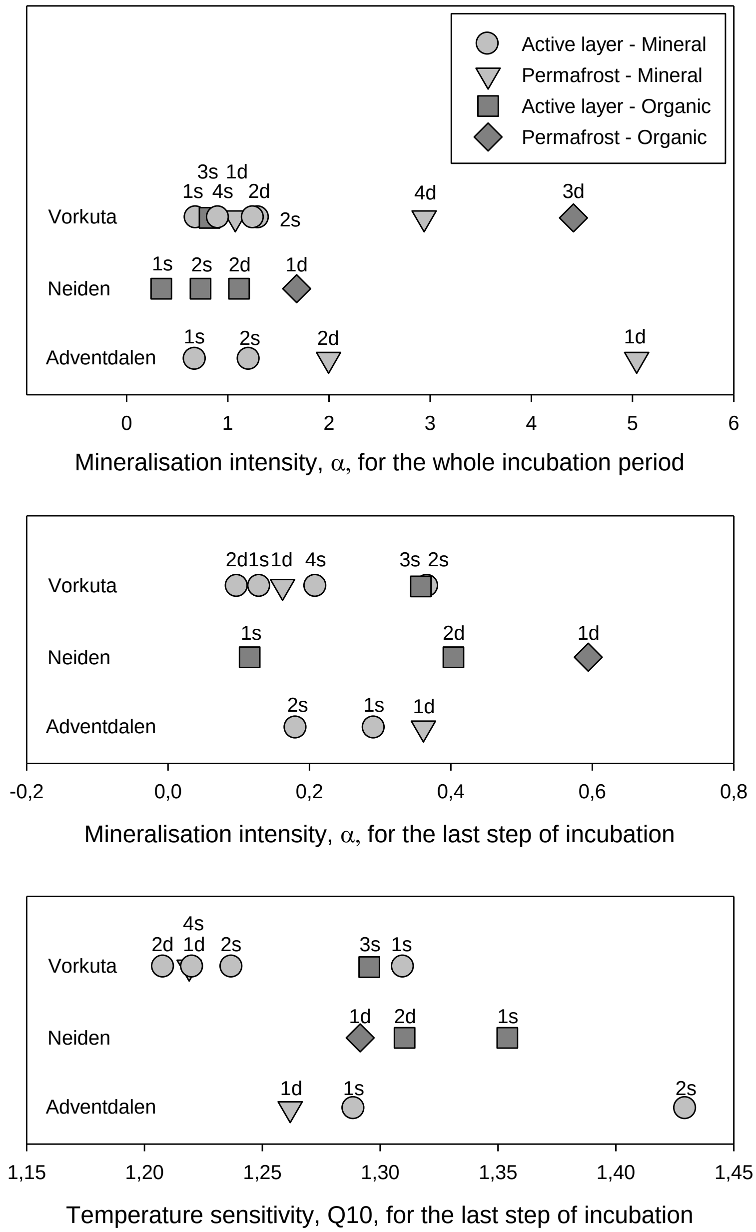

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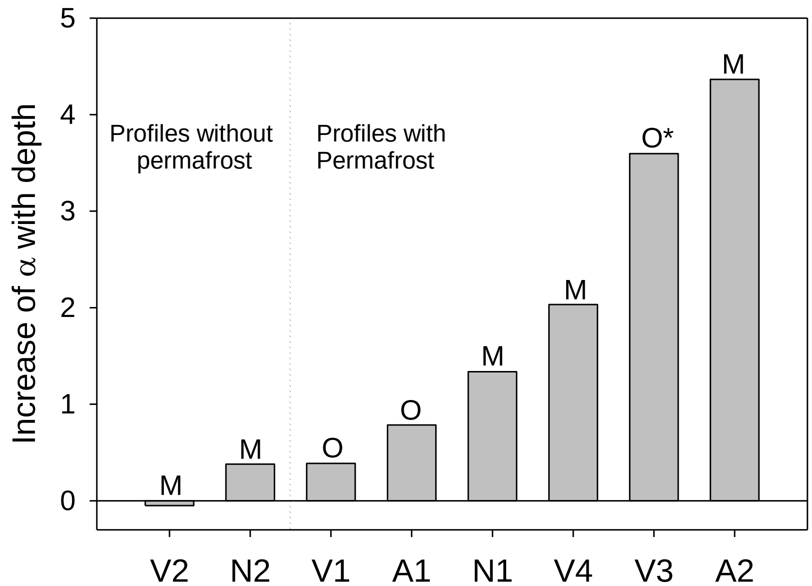

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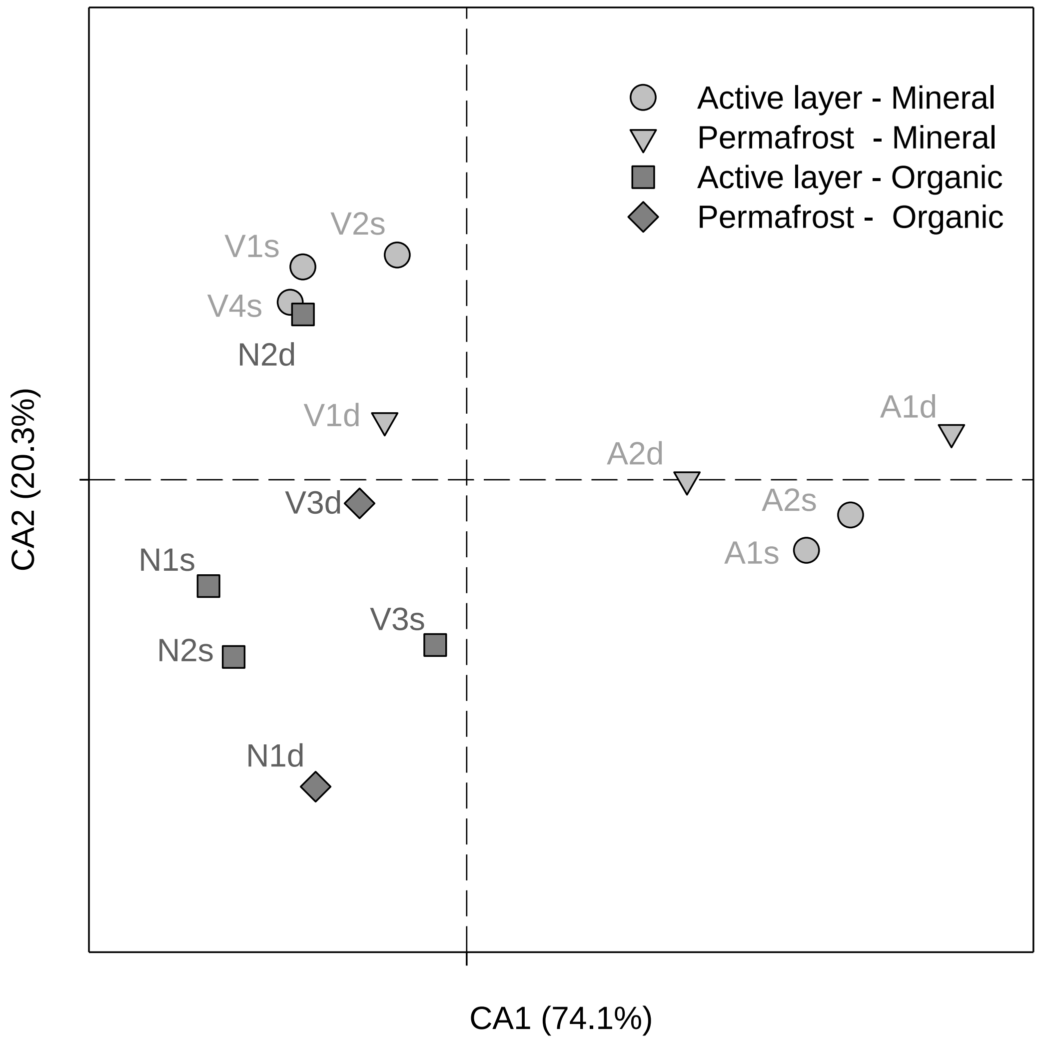

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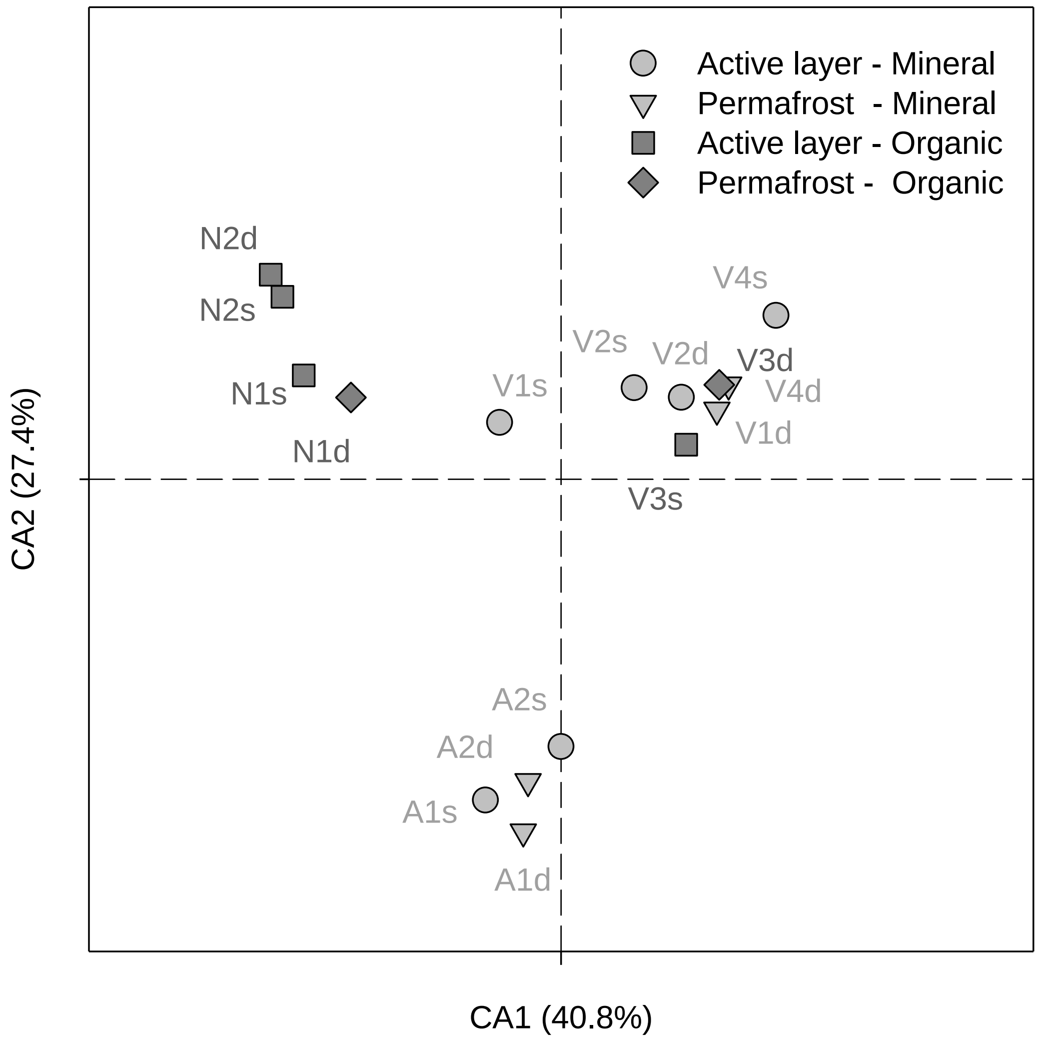

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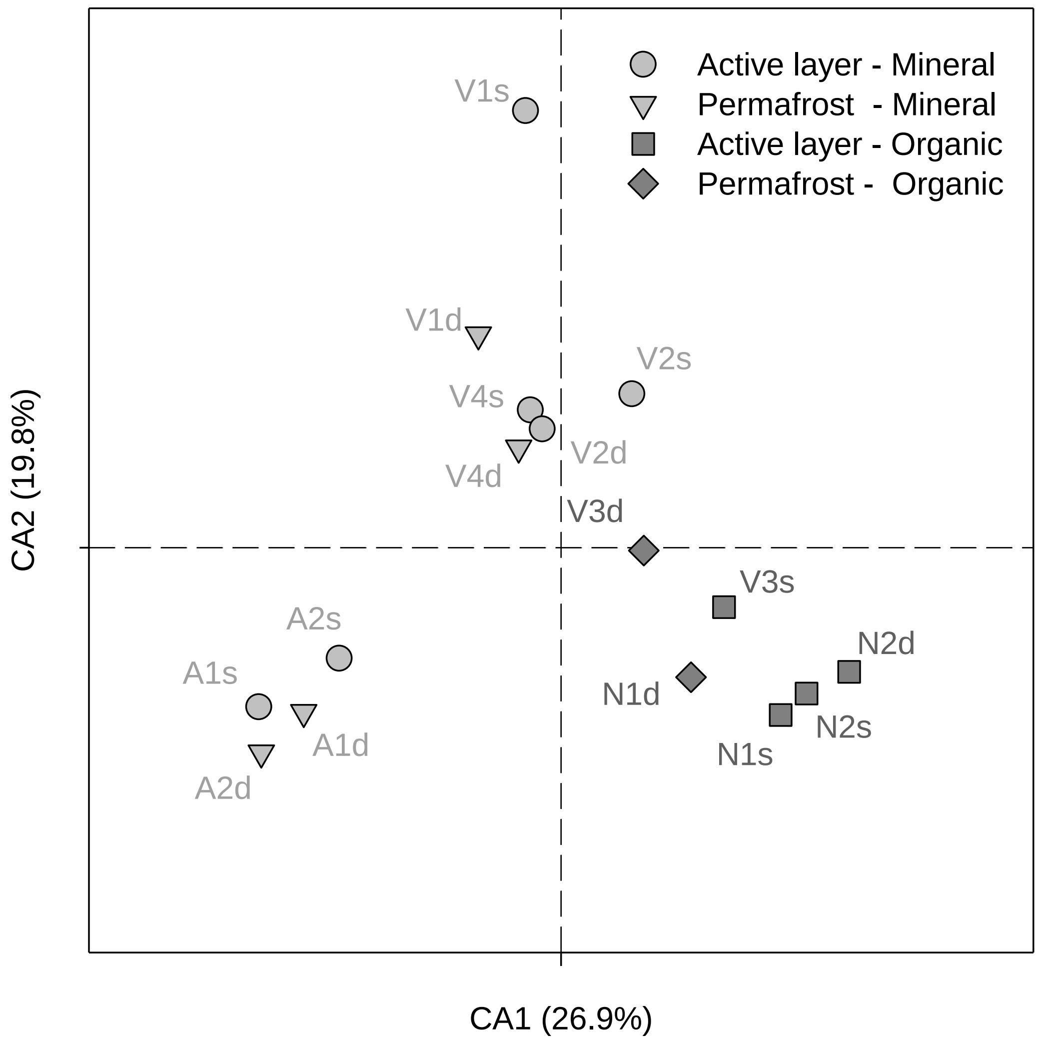

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