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Soil Organic Matter Characteristics in Sporadic Permafrost-affected Environment (Creux du Van, Switzerland)

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Abstract

In permafrost-affected sites, soil forming processes appear to be closely connected with organic matter (OM) accumulation. In this work OM composition and nutrient availability has been evaluated in a frost-affected soil located at 1200 m a.s.l. in Creux du Van (Switzerland), where patches of stunted Norway spruce trees adjacent to tall trees have been ascribed to the presence of sporadic alpine permafrost. Soil samples were collected under the stunted forest and in the adjacent tall forest and characterized for their chemical and physical characteristics. The main C and N forms have been determined and characterized.

Under the stunted forest the soil samples showed a high total organic C/total N (TOC/TN) ratio and scarce microbial activity; humification processes were limited and humic acids revealed little oxidation, scarce incorporation of N-containing moieties, and high enrichment of lipids. ¹⁴C dating revealed the presence in the bulk samples of young organic material mixed with relatively old humic acids, probably due to cryoturbation processes. These latter processes appeared also responsible for the arrival of fresh litter material from Oi and Oe horizons into the Oa horizon of the stunted forest and for the consequent genesis of humic substances from a mix of old and fresh residues.

From our findings there seems to exist a reciprocal influence of vegetation quality on the OM composition, and of OM decomposition on nutrition, as driven by the microclimatic conditions and physical processes, which in turn may contribute to keep the soil at an unstable developmental stage and limit the spruce growth.

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Introduction

Permafrost is defined as a thermal condition in which soil materials, sediments, or rocks remain below 0 °C for two or more years in succession (IUSS Working Group WRB, 2006). In cold environments soil-forming processes appear to be closely connected with organic matter (OM) accumulation (Richard, 1961; Duchaufour, 1976; Campbell and Claridge, 1987; French, 1996). The strong relationship between soil OM accumulation and climate has been investigated by several authors (i.e. Post et al., 1982; Trumbore et al., 1996). While soil OM content is correlated positively with precipitation and negatively with temperature (Jenny, 1980), in permafrost-affected soils, OM is preserved due to the prevailing cold and wet conditions that constrain or slow down its decomposition (Hobbie et al., 2000; Weintraub and Schimel, 2003; Uhlířová et al., 2007). In these environments, besides temperature and oxygen limitation due to reducing conditions, the quality of the organic substrate, which is in turn a function of plant species and growth forms (Kögel-Knabner, 2002), may drive the decomposition dynamics. Several studies indicated that the effect of plant composition on degradation may be large compared with the influence of temperature in cold environments, probably reflecting the diversity of growth forms observed in these areas (Hobbie et al., 2000). Woody stems, mosses, lichens, and coniferous residues decompose more slowly than those of deciduous and herbaceous species (Kögel-Knabner, 2002; Dorrepaal et al., 2005; Lang et al., 2009).

The organic material accumulated in permafrost-affected soil is thus mainly in forms of poorly decomposed plant remains, less humified (Dalias et al., 2001) and with higher TOC/TN ratios (Ping et al., 1997) compared with the soils of temperate regions. Physical and chemical analyses indicate that a large proportion of OM in permafrost is comprised of a pool of labile compounds characterized by high biodegradability and accumulates mainly in the NaOH non-extractable fraction (Ping et al., 1997). In warmer ecosystems, this organic pool may be easily susceptible to mineralization, as observed in laboratory incubations (Mikan et al., 2002; Weintraub and Schimel, 2003; Shaver et al., 2006; Uhlířová et al., 2007), and could yield promptly available nutrient forms for plants and microorganisms (Schmidt et al., 1999).

Permafrost-affected soils are mostly located at high latitudes in the northern continuous permafrost zone, but discontinuous alpine permafrost may exist at much lower latitudes in high elevation areas. Below the timberline, sporadic permafrost is assumed to exist only in scree slopes located at the foot of high cliffs, in very shaded sites (Kneisel et al., 2000).

An example of a cold site below the limit of discontinuous alpine permafrost is Creux du Van, located in the Jura Range in northwestern Switzerland. In this site, the presence of sporadic permafrost in the form of ice lenses is reported to keep the soil temperature 2–3 °C colder than surrounding areas not affected by ice, although air temperature is similar and warm in the growing season (Delaloye et al., 2003; Körner and Hoch, 2006; Freppaz et al., 2008). The area is characterized by a natural amphitheater,

which has attracted many scientists (Lesquereux, 1844; Duchaufour, 1976, 1983; Gobat et al., 2004) due to the presence of patches of peculiarly stunted Norway spruce (*Picea abies* L. Karsten) trees. The limited plant growth has been linked for many years only to the large difference between air and soil temperature due to the presence of permafrost (Richard, 1961). Recent works have attributed the reduced plant growth mainly to plant physiological stresses, “since roots are cold but not shoots” (Körner and Hoch, 2006), and to asynchrony in the early spring between the availability of critical resources and their utilization by plants, with potential loss of nutrients before the plants start their vegetation growth (Freppaz et al., 2008).

As the nutrient cycling is tightly linked to OM characteristics and dynamics, the present study aimed to investigate the quality of soil OM accumulated in this anomalous frost-affected environment in order to evaluate a possible role of OM dynamics on the limited plant growth. To reach this goal, OM extracted from the permafrost-affected soil was characterized and compared to that from the surrounding areas not affected by permafrost and covered by tall spruce forest.

Materials and Methods

SITE, SOIL DESCRIPTION, AND SAMPLING

The study was carried out in Creux du Van, Swiss Jura (46°56'N, 6°44'E) (Fig. 1). The site is a talus slope located at the bottom of a cirque facing east-northeast between 1170 and 1300 m a.s.l. (Fig. 1). The cirque is closed from its southern to western rim by a 100- to 150-m-high cliff of hard limestone marl, and fallen blocks have built up a well-sorted talus slope at the base of the cliff. The mean annual air temperature is +5.5 °C (Delaloye and Reynard, 2001), and the mean annual precipitation is around 1600 mm.

The very steep and unstable uppermost part of the scree consists of gravels without soil formation, while the lower portion, characterized by gentle slope and higher stability, is comprised of large blocks of hard limestone covered by an organic soil (Gobat et al., 2004).

A discontinuous permafrost table, present under the blocks in the lower part of the scree, is reported to be maintained by the advective energy fluxes due to air density contrasts between the open space among the blocks and the atmosphere (Delaloye et al., 2003). The different ground thermal conditions are also indicated by the distribution of vegetation belonging to the *Tofieldio-Picetum* association on the talus slope: stunted spruces (*Picea abies* L. Karsten) in several patches of the lower part of the talus slope where ice lenses are present, and tall spruces in the portion of the slope free of ice. The understory is dominated by *Vaccinium myrtillus* and mosses. Due to the small diameter of the ice lenses (30–60 m), tall and stunted trees occur in adjacent stands with a sharp transition (Fig. 1).

The soils of the two sites are comprised of a thin unaltered organic horizon (Oi), followed by a semi-altered organic horizon (Oe, about 10 and 30 cm in the stunted and in the reference forest, respectively) and an Oa horizon, which, in turn, rest on the blocks of hard limestone eroded from the escarpment and with large interstices. The Oa horizon under the stunted forest is of variable depth ranging between 10 and 45 cm, while in the site free of ice and covered by the tall forest the thickness ranges from about 35 to 55 cm.

In the stunted forest the Oa horizon is characterized by higher moisture content related to the presence of permafrost; nevertheless, the advective air fluxes maintain the soil more oxygenated

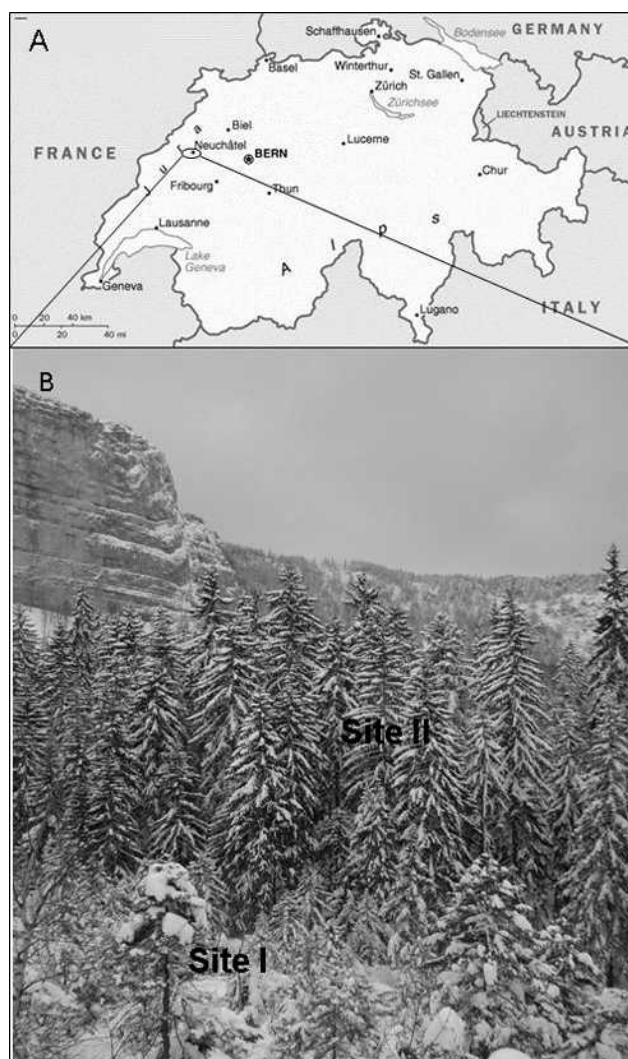


FIGURE 1. (A) Map of Switzerland with the study area indicated (46°56'N, 6°44'E), and (B) the study area (Creux du Van) and the position of the sampling sites within talus slope.

than that under the reference forest (Freppaz et al., 2008). The soil under the stunted trees is classified as Cryic Histosol (IUSS Working Group WRB, 2006) or Lithic Sapristel (Soil Survey Staff, 2003). The soil under the reference trees is classified as Sapric Histosol (IUSS Working Group WRB, 2006) or Lithic Cryosaprist (Soil Survey Staff, 2003).

Soil samples were collected during November 2001 from two sites corresponding to the prevailing *Picea abies* growth forms: site I, the stunted forest, and site II, the reference forest. Ten soil samples were collected from the Oa horizon of each site using a soil corer (diameter: 10 cm; volume: 500 mL). The collected samples of each site were pooled together and subdivided into three sub-samples. Each sub-sample was placed in a plastic bag and maintained at low temperature (0 °C) to limit biological activity during transport to the laboratory. An aliquot of each sub-sample was oven dried at 40 °C to constant weight, ground, and sieved through 2 mm to carry out the chemical analyses. The remaining sample was stored at 0 °C in order to maintain it at the same temperature recorded in the field during November (Freppaz et al., 2008). For each site, three additional samples were collected and used as such for the measurement of the bulk density. Skeleton was absent in all Oi, Oe and Oa horizons.

The bulk density was computed by the formula:

$$BD = \text{weight} / \text{volume}, \quad (1)$$

where *weight* is the 105 °C dry weight of the intact soil cores, and *volume* is 500 mL. Total soil carbon and nitrogen (TN) were measured using a Thermoquest NC 2005 combustion analyzer. CaCO₃ content was determined by a Scheibler's calcimeter. The total organic C (TOC) was calculated by difference between total and inorganic C. The pH in water was determined potentiometrically (1:20 soil-water suspension).

To determine NH₄⁺ and NO₃⁻ concentrations, 10 g of sample were added to 50 mL of 0.5M K₂SO₄ solution and shaken for 1 h, centrifuged, and filtered. Ammonium in K₂SO₄ extracts was diffused into 0.01M H₂SO₄ solution after treatment with magnesium oxide (Bremner, 1965) and the trapped NH₄⁺ was determined colorimetrically (Crooke and Simpson, 1971). Nitrate in the same extracts was determined colorimetrically as NH₄⁺ after reduction with Devarda alloy. Organic nitrogen (N_{org}) was determined as the difference between total N and the inorganic N species.

For the determination of the dissolved organic compounds, 10 g of sample was shaken with 100 mL 0.5M K₂SO₄ solution for 1 h and the suspension filtered through 0.45 µm under suction. Total dissolved N (TDN) in the extracts was measured as NH₄⁺ after oxidation of aliquots of extracts with alkaline persulfate and subsequent reduction with Devarda alloy (Williams et al., 1995). Dissolved organic N was calculated as DON = TDN - (NH₄⁺ + NO₃⁻). Dissolved organic carbon (DOC) in the 0.5M K₂SO₄ suspension was measured by the Walkley and Black wet oxidation method (Nelson and Sommers, 1982).

To measure microbial biomass C and N, a set of samples was fumigated overnight with chloroform and extracted with 0.5M K₂SO₄ solution in parallel with a set of unfumigated samples (Williams and Sparling, 1988). Biomass C and N values were calculated from the flushes of extractable C and N using the recovery factors of 0.45 for C (Sarathchandra et al., 1989) and 0.54 for N (Brookes et al., 1985).

The content of lipids and chlorophyll was determined by using the method described by Stevenson (1994). The two components were extracted by hot distillation from 3 g of soil treated with an ethanol-benzene (2:1) solution. The lipid content was determined by weight after solvent evaporation. The chlorophyll content was determined measuring optical density of the extracting solution at 666 nm (Spectracomp 602; Carlo Erba, Milan, Italy).

SOIL ORGANIC MATTER FRACTIONATION AND CHARACTERIZATION

Humic acids (HA) and fulvic acids (FA) were extracted and purified following the procedure described by Schnitzer (1982). Briefly, HA and FA were extracted with 0.1M NaOH solution (soil:liquid ratio 1:10) under N₂. After 24 h of shaking, the alkaline supernatant was separated from the soil residue by centrifugation at 1516 g for 20 min and treated with 6M HCl solution to induce the precipitation of HA. The supernatant containing FA was separated from the precipitate (HA) by centrifugation at 1516 g for 15 min. The HA were then re-dissolved in 0.1M NaOH solution, shaken for 4 h under N₂, and the suspended solids were removed by centrifugation. The C content of raw FA and HA was determined on an aliquot of the obtained solutions by the Walkley and Black method (Nelson and Sommers, 1982). The non-

extractable carbon (NE-C) was determined by difference between total carbon and the HA+FA carbon content.

The HA solution was acidified again with 6M HCl to pH 1 and HA separated by centrifugation. Humic acids were demineralized by shaking overnight with a 0.1M HCl:0.3M HF solution (solid:liquid ratio 1:1) and then washed with deionized water until the solution pH was 3. Fulvic acids were purified by using XAD-8 and IR-120 resins. Both HA and FA solutions were freeze-dried.

Humic acids were characterized for their elemental composition (C, N, H, S) by a CHN-600 combustion analyzer (LECO, St. Joseph, Michigan, U.S.A.), while the O content was calculated by difference. The obtained data were corrected for ash and moisture content.

The E₄/E₆ ratio was determined following the procedure described by Chen et al. (1977). The samples were dissolved in 50 mL of 0.05N NaHCO₃ solution and the optical density was measured at 450 and 650 nm.

Fourier-Transform Infrared (FT-IR) spectra were obtained using a Perkin Elmer 16F PC FT-IR spectrophotometer. The pellets were prepared by pressing under vacuum a mixture of 1 mg of organic material with 400 mg of KBr (spectrometry grade). Spectra were acquired at 4 cm⁻¹ resolution and 64 scans were averaged.

RADIOCARBON MEASUREMENTS

Natural abundance of ¹⁴C was obtained by accelerator mass spectrometry (AMS) at the Keck Carbon Cycle Accelerator Mass Spectrometry Laboratory, Earth System Science Department, University of California, Irvine (U.S.A.). It was expressed in Δ¹⁴C, the ‰ deviation from the ¹⁴C/¹²C ratio of oxalic acid standard in 1950 (Modern) corrected for a δ¹³C of -25‰, which takes into consideration the mass dependent isotopic fractionation effects (Stuiver and Polach, 1977). The measurements were run on bulk samples and humic acids. To avoid possible interference of inorganic C, the bulk samples were cleared up of small fragments of limestone by using tweezers under a magnifying lens and then kept in a desiccator in the presence of concentrated HCl for a week to remove the carbonate-C.

On the basis of the radiocarbon data and according to the model of Trumbore et al. (1996) and Gaudinski et al. (2000), reported in detail in Agnelli et al. (2002), we calculated the mean residence time (MRT) of the C in the analyzed samples.

STATISTICS

The mean of three analytical replicates (with the exception of radiocarbon measurements, where *n* = 2) and the standard error were calculated for the quantitative analyses (Webster, 2001). The propagation error technique (Skoog and West, 1987) was used to calculate the standard errors of the values obtained by subtraction.

Results

SOIL PHYSICAL AND CHEMICAL CHARACTERISTICS

The Oa horizons of the two soils had a similar bulk density (0.2 kg dm⁻³). The pH was higher in the stunted forest (site I, pH = 7.2) compared to the reference site (site II, pH = 6.4). The total organic C content (TOC) and the dissolved organic C content (DOC) were comparable in the two sites (Table 1), whereas the total nitrogen (TN) and the dissolved organic N (DON) were higher in site I than in site II. The TOC/TN ratio was 24 under the stunted forest and 29 under the reference forest. In terms of stock,

TABLE 1

Organic C forms (total organic C—TOC, dissolved organic C—DOC, microbial biomass C— C_{micr} , extractable C in 0.1 M NaOH solution— $C_{\text{HA+FA}}$, C content of fulvic and humic acids— C_{FA} and C_{HA} , and non-extractable C— C_{NE}) and N forms (total N—TN, dissolved organic N—DON, microbial biomass N— N_{micr} , extractable N in 0.1 M NaOH solution— $N_{\text{HA+FA}}$, N content of fulvic and humic acids— N_{FA} and N_{HA} , and non-extractable N— N_{NE}) in the Oa horizons of the stunted forest (site I) and reference forest (site II) located in Creux du Van (CH). Numbers in parentheses are the standard errors ($n = 3$).

	Site I		Site II	
	soil (g kg ⁻¹)	TOC (%)	soil (g kg ⁻¹)	TOC (%)
TOC	379 (1.2)		347 (1.5)	
DOC	16.9 (0.04)	4.5	15.0 (0.07)	4.3
C_{micr}	1.14 (0.20)	0.3	2.80 (0.15)	0.81
$C_{\text{HA} + \text{FA}}$	75.6 (1.40)	19	80.9 (1.25)	23.3
C_{FA}	33.6 (0.02)	9.0	24.0 (0.10)	6.91
C_{HA}	42.0 (1.38)	11.1	57.0 (1.15)	16.4
C_{NE}	263 (1.24)	69.6	238 (1.35)	68.7
	soil (g kg ⁻¹)	TN (%)	soil (g kg ⁻¹)	TN (%)
TN	16.0 (0.31)		12.0 (0.25)	
DON	0.44 (0.08)	2.8	0.19 (0.07)	1.6
N_{micr}	0.12 (0.04)	0.7	0.72 (0.05)	5.9
$N_{\text{HA} + \text{FA}}$	3.7 (0.04)	23.1	5.3 (0.03)	44.2
N_{FA}	1.7 (0.01)	10.9	1.0 (0.02)	8.3
N_{HA}	2.0 (0.03)	12.2	4.3 (0.01)	35.8
N_{NE}	11.7 (0.31)	73.4	6.51 (0.45)	54.2
TOC/TN	24		29	

by considering bulk density and horizon thickness, the amount of C accumulated in the Oa horizon of the stunted forest was much lower than that in the reference site with mean values of 19 and 31 kg m⁻², respectively.

Microbial C and N contents were much lower under the stunted forest than under the reference forest, especially if expressed as percent of the TOC and TN (Table 1). The amount of C and N extractable in 0.1M NaOH solution ($C_{\text{HA+FA}}$ and $N_{\text{HA+FA}}$) was less abundant under the stunted forest and represented by similar amounts of humic and fulvic acids (HA/FA = 1.25) while, in the reference site, HA prevailed distinctly over the FA, leading to a HA/FA ratio of 2.43. The non-extractable organic material was characterized by larger amounts of C and N (Table 1) and a lower TOC/TN ratio (22.5 and 31.0) in the stunted and reference forest, respectively.

The amount of ethanol:benzene extractable lipids in the bulk soil of the stunted forest was 20.9 g kg⁻¹ soil, corresponding to 6.6% of TOC. In the reference site the amount of lipids was less than halved, 8.49 g kg⁻¹ soil, corresponding to 3.2% of TOC. Chlorophyll

content was substantially higher in site I (36.0 mg kg⁻¹) than in site II (11.4 mg kg⁻¹).

HUMIC SUBSTANCES

The humic acids of the stunted forest presented higher C and H contents and lower O and N contents than those of the reference site (Table 2). Consequently, HA from site I had higher atomic C/N and H/C ratios, and a lower atomic O/C ratio. Fulvic acids appeared more homogeneous between the two sites, although those from the stunted forest had a slightly larger incorporation of N and lower O/C ratio than those extracted from the site II. The E_4/E_6 ratio did not show any relevant difference between the two HA and the two FA (Table 2).

The FT-IR spectra of HA (Fig. 2) showed a large peak at 3368 cm⁻¹ due to stretching of hydroxyl groups, bands at 2923 cm⁻¹ and 2850 cm⁻¹ (aliphatic C-H stretching), slightly more evident in the HA spectrum of site I. The band at 1720 cm⁻¹, due to C=O stretching of different groups (mainly carboxyls), was more intense in the HA of the stunted forest than in those of the reference site. Conversely, the band at 1630 cm⁻¹ (C=C of aromatic groups) was more pronounced in the HA of site II. HA showed a different distribution of carbohydrate forms: the more pronounced peak at 1220 cm⁻¹ (C-OH stretching) in site I may suggest a larger presence of mono- and oligosaccharides, while the sharper band at 1033 cm⁻¹ in site II may be an index of greater presence of polysaccharides. However, the stretching of Me-O at this frequency cannot be ruled out, as deduced also by the higher presence of ash in HA from site II (Table 2).

The spectra of FA (Fig. 2) had a less pronounced band than HA at 2923 cm⁻¹, due to aliphatic C-H stretching. The peak at 1720 cm⁻¹ was more marked in the fulvic fraction of site II, indicating the presence of more acidic compounds than in the stunted forest.

The interpretation of the FT-IR spectra is based on data reported in Celi et al. (1997), and references therein.

¹⁴C DATING

The measurement of ¹⁴C natural abundance in the bulk samples (Table 3) gave larger values of $\delta^{14}\text{C}$ for site I than for site II (-6.9‰ vs. -66.5‰, respectively). The ¹⁴C-based age of the organic material in the bulk soil from site I was not determinable, since the value of $\delta^{14}\text{C}$ indicated the presence of ¹⁴C produced by nuclear weapons testing, meaning that a considerable amount of the C in the analyzed material was fixed by plants in recent times (after 1950). Conversely, the mean radiocarbon age of the organic material in the bulk soil from site II was 500 years BP (Before Present). The calculated mean residence time (MRT) of the organic pool from site I gave lower values than that from site II

TABLE 2

Elemental composition (percentage expressed on a moisture- and ash-free basis), atomic ratio, optical density at 450 and 650 nm of alkaline HA and FA solution (E_4/E_6 ratio), and ash content of humic acids (HA) and fulvic acids (FA) extracted from the Oa horizons of the stunted forest (site I) and reference forest (site II) located in Creux du Van (CH).

		C	H	N	S	O					
		(%)					H/C	C/N	O/C	E_4/E_6	Ash (%)
HA	Site I	55.0	6.5	2.6	0.4	35.5	1.4	24.5	0.51	5	0.0
	Site II	49.0	4.7	3.7	0.0	42.7	1.1	15.6	0.70	4	2.4
FA	Site I	49.2	5.4	2.5	0.3	42.7	1.3	22.9	0.65	11	1.0
	Site II	47.9	4.7	2.1	0.3	45.0	1.2	27.2	0.72	10	1.1

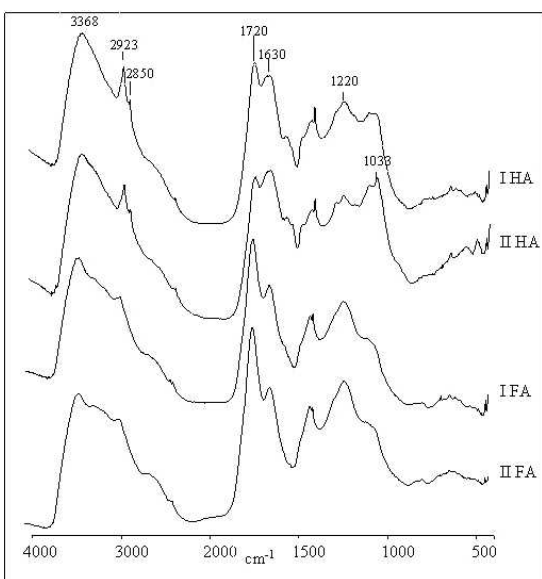


FIGURE 2. FT-IR spectra of HA and FA extracted from the Oa horizons of the stunted forest (site I) and reference forest (site II) located in Creux du Van (CH).

(350 vs. 734 years, respectively). Humic acids had a lower abundance of radiocarbon compared with the bulk soils, confirming both the heterogeneity of OM and the relative recalcitrance of the HA fraction. Also in this case, however, the HA from site I had larger abundance of ^{14}C than the HA from site II and, consequently, a lower age and MRT (Table 3).

Discussion

The microclimatic conditions determined by the presence of permafrost lenses seem to affect vegetation growth and soil formation, with sharp transition between the stunted forest and the adjacent tall forest site (Delaloye et al., 2003; Körner and Hoch, 2006; Freppaz et al., 2008). The colder and moister conditions due to the presence of the ice lenses may be the first cause for the formation of short and sparse spruce trees, and have also led to a different understory represented mostly by *Sphagnum* and *Vaccinium*, compared to the surrounding area, where the *Sphagnum* was almost absent. Under these conditions, the Oa horizon of both sites was characterized by a slightly degraded organic material, as suggested by the high TOC/TN ratio, although this ratio was lower in the stunted forest compared to the reference site. The high accumulation of N, as well as of lipids and chlorophyll, could be due to the particular adaptation of spruce to the cold environment, which results in a lower growth, together with a greater photosynthesis, larger production of chlorophyll and lipids, and a higher N incorporation in the needles (Oleksyn et al., 1998; Weih and Karlsson, 2001). This behavior has been reported for high elevation treeline trees and for stunted shrubs in the transition zone between forest and prairie, and attributed to a lack of “dilution by growth” (e.g. Tschager et al., 1982; Körner, 1989) due to a limitation caused by the low temperature on several physiological processes, such as mitochondrial respiration (Dahl, 1986) and protein synthesis (Körner, 1998). The higher amount of lipids found under the stunted forest can be responsible also for the processes of encapsulation of proteins and amino acids into OM (Zang et al., 2000; Spaccini et al., 2002), by further favoring N preservation. Moreover, N accumulation in the soil of site I, together with a low C content

TABLE 3

$\Delta^{14}\text{C}$, ^{14}C -based age and mean residence time (MRT) of bulk soil and humic acids (HA) of the Oa horizons of the stunted forest (site I) and reference forest (site II) located in Creux du Van (CH). The data are reported as the mean of two replicates (reported in parentheses).

	$\Delta^{14}\text{C}$ (‰)	^{14}C age (years BP)	MRT (years)
<i>Bulk soil</i>			
Site I	-6.9 (-4.6; -9.2)	n.d.	350 (339–361)
Site II	-66.5 (-64.1; -68.9)	500 (480–520)	734 (715–753)
<i>Humic acid</i>			
Site I	-76 (-71.9; -80.1)	585 (550–620)	810 (774–844)
Site II	-117.2 (-118.1; -116.3)	953 (960–945)	1180 (1189–1172)

BP: before present; n.d.: not determinable.

could be attributed to a selective degradation of easily decomposable O-containing compounds (Saiz-Jimenez, 1996). This would reduce the degradation of N-containing products that mostly remained in the non-extractable organic fraction. However, in agreement with the results observed in the superficial organic layers of tundra soils (Dai et al., 2002; Uhlřová et al., 2007), the high amounts of DON forms found in the stunted forest may be due to a limited microbial activity, as suggested by the scarce amounts of microbial C biomass compared to the reference site. The low amount of microbial C under the stunted forest, even lower than that reported for arctic soils (Schmidt et al., 1999), could be related also to the presence of *Sphagnum* spp. that might produce allelopathic compounds with a microbial inhibitory effect (Painter, 1991). The small amount of humic C and the low HA/FA ratio should confirm the limited decomposition and humification processes of the organic material accumulated under the stunted forest, according to some authors who found that the HA/FA ratio was generally lower in less developed soils (Kononova, 1966; Ping et al., 1997; Dai et al., 2002). To evaluate the degree of OM decomposition we plotted the Van Krevelen diagrams (Durand and Monin, 1980; Haumaier and Zech, 1995) of atomic H/C versus atomic O/C ratios of HA and FA from the two sites. From these diagrams (Fig. 3), the HA extracted from site I showed a lower degree of oxidation and degradation (higher H/C and lower O/C) compared to the HA from site II where demethylation and oxidation processes seem to drive their formation (Barančiková et al., 1997; Orlov et al., 1987). To a lesser extent, fulvic acids followed the same trend.

Compared to site II, the humic substances extracted from the Oa horizon of site I had a dominance of the aliphatic component with a large presence of material characterized by a low incorporation of O- and N-containing functional groups that, together with the lower amount of N-containing residues in the HA structure (12.2 and 35.8% of the TN, respectively; Table 1), should confirm the limited transformation of OM under the stunted forest. The low incorporation of N in the humic structure suggested a low biological activity (Agnelli et al., 2002) in soil I, in agreement with previous findings which showed that N mineralization in the stunted forest was confined to very labile compounds (Freppaz et al., 2008), thus leaving the most part of N in the non-extractable fraction or even in dissolved forms.

Consistent with the larger amount of lipids in the bulk Oa horizon, the HA and FA from site I were richer in alkyl compounds (higher H/C) compared with those of site II. This could be due to a major proportion of lipids with a high resistance to degradation produced by the vegetation growing in the colder site and with a short vegetative period (Johnson and Damman, 1991; Oleksyn et

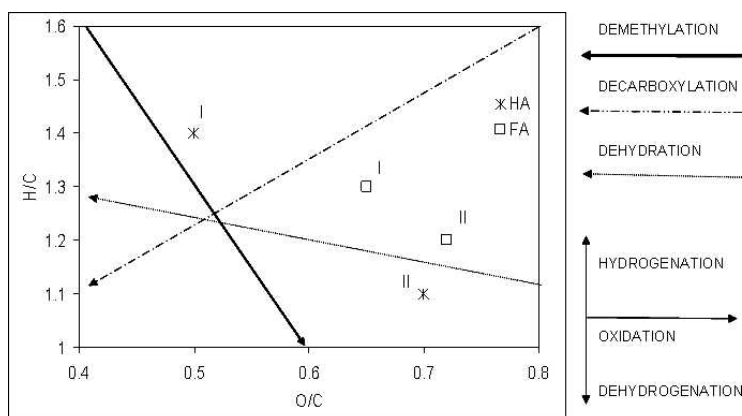


FIGURE 3. Van Krevelen diagram of HA and FA extracted from the Oa horizons of the stunted forest (site I) and reference forest (site II) located in Creux du Van (CH).

al., 1998). Dai et al. (2002) found a higher percentage of lipids in three Arctic Gelisols compared to a Mollisol. Moreover, lipids might accumulate in the humic substances as a result of selective preservation of waxes, paraffins, and other compounds hard to decompose (Ziegler and Zech, 1989; Cerli et al., 2008). In cold environments, these recalcitrant compounds may dominate the OM pools, since decomposers break down preferentially the most labile material (Hobbie et al., 2000).

From these results it appears that in the stunted forest the more humified fraction is composed of raw, undegraded and slightly oxidized compounds. However, ^{14}C dating highlighted important differences between the bulk samples and the extracted HA, especially in the stunted forest. In both soils, the humic fractions were relatively older than the bulk organic pool, which appeared to be comprised of a heterogeneous mix of fresh and aged materials. Since small amounts of very old C can greatly influence the ^{14}C signature and/or the estimated age of the samples (Paul et al., 1997), it is likely that the bulk OM was comprised of a very high proportion of fresh residues. Consequently, the higher $\Delta^{14}\text{C}$ signature obtained for the bulk soil OM of site I compared with that of site II should indicate the presence of a lower amount of humified substances in the organic pool of the soil under the stunted forest. This fact, confirmed also by the $\text{TOC}/\text{C}_{\text{HA+FA}}$ ratios (5.01 and 4.2 for site I and II, respectively), corroborated the hypothesis of a slower OM cycling in the permafrost-affected soil. However, besides biochemical and chemical processes, other phenomena may be involved in the organic matter cycling. It should be considered that in areas dominated by permafrost, cryoturbation may be an additional process that affects the soil. This occurs under the influence of cryostatic pressures, gravity, and downward movements during the thawing period of the permafrost active layer, with consequent transfer of OM from superficial horizons into permanently frozen horizons (Bockheim and Tarnocai, 1998; Grieve, 2000; Dai et al., 2001). In site I, these processes may have favored the translocation of fresh plant remains from the upper Oi and Oe horizons into the Oa horizon (Freppaz et al., 2008) and the mixing with the more stabilized fraction. We have to consider also that the Oa horizon rests on large blocks with large interstices, allowing downwards movement and deposit of the Oa material and renewal of the upper part of the horizon. The radiocarbon, chemical, and spectroscopic findings of HA could confirm the above hypothesis of an arrival of fresh litter material from Oi and Oe horizons into the Oa horizon, where the humic substances derived from a mix of old and fresh residues (with relatively high abundance of ^{14}C) were subjected to low-intensity and temperature-limited humification processes. The absence of cryoturbation in the site II soil may limit the incorporation of fresh plant remains from

the Oi and Oe horizons into the Oa material; this will constrain the “rejuvenation” of the substrates from which HAs are synthesized.

Conclusion

At Creux du Van, the complex interaction between microclimate, vegetation, and nutrient cycling may lead to important differences in soil OM characteristics in the permafrost-affected soil under the stunted forest compared to those of the surrounding area.

The organic material accumulated in the permafrost-affected soil was characterized by remains at a low degree of decomposition, with a larger percentage of chlorophyll, lipids, and N-containing compounds compared with the reference site. This may be the result of different combined phenomena produced by critical pedoclimatic conditions such as the development of a different plant community, changes in the spruce composition and anatomy, a low biological activity, and pedoturbations due to the presence of permafrost.

Organic matter characteristics clearly indicated that under the stunted forest humification and mineralization processes were very limited. A soil temperature slightly colder than the surrounding site may strongly reduce OM decomposition and transformation. Even the organic fractions that should be expected to be more humified, such as the humic acids, were comprised of raw undegraded and slightly oxidized compounds.

Soil properties and development in this environment thus reflect the reciprocal influence of vegetation quality on OM composition and dynamics, and of OM decomposition on nutrient availability, as driven by the microclimatic conditions. The equilibrium that could be reached among these processes may be strongly affected or even disrupted by physical events linked to the presence of the permafrost lenses, such as soil cryoturbation, which keep the soil under the stunted forest at an unstable developmental stage.

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References Cited

- Agnelli, A., Trumbore, S. E., Corti, G., and Ugolini, F. C., 2002: The dynamics of organic matter in rock fragments in soil investigated by ^{14}C dating and measurements of ^{13}C . *European Journal of Soil Science*, 53: 147–159.

- Barančiková, G., Senesi, N., and Brunetti, G., 1997: Chemical and spectroscopic characterization of humic acids isolated from different Slovak soil types. *Geoderma*, 78: 251–266.
- Bockheim, J. G., and Tarnocai, C., 1998: Recognition of cryoturbation for classifying permafrost-affected soils. *Geoderma*, 81: 281–293.
- Bremner, J. M., 1965: Inorganic forms of nitrogen. In: Black, C. A. (ed.), *Methods of Soil Analysis, Part 2. Chemical Methods*. Madison, Wisconsin: American Society of Agronomy, 1179–1206.
- Brookes, P. C., Landman, A., Pruden, G., and Jenkinson, D. S., 1985: Chloroform fumigation and the release of soil nitrogen: a rapid direct extraction method to measure microbial biomass nitrogen in soil. *Soil Biology and Biochemistry*, 17: 837–842.
- Campbell, I. B., and Claridge, G. G. C., 1987: *Antarctica: Soils, Weathering Processes and Environment*. Amsterdam: Elsevier.
- Celi, L., Schnitzer, M., and Nègre, M., 1997: Analysis of carboxyl groups in soil humic acids by a wet chemical method, Fourier-transform infrared spectrophotometry, and solution-state carbon-13 nuclear magnetic resonance. A comparative study. *Soil Science*, 162: 189–197.
- Cerli, C., Celi, L., Kaiser, K., Guggenberger, G., Johansson, M.-B., Cignetti, A., and Zanini, E., 2008: Changes in humic substances along an age sequence of Norway spruce stands planted on former agricultural land. *Organic Geochemistry*, 39: 1269–1280.
- Chen, Y., Senesi, N., and Schnitzer, M., 1977: Information provided on humic substances by E4/E6 ratios. *Soil Science Society of America Journal*, 41: 352–358.
- Crooke, W. M., and Simpson, W. E., 1971: Determination of ammonium in Kjeldahl digests of crops by an automated procedure. *Journal of Science and Food Agriculture*, 22: 9–10.
- Dahl, E., 1986: Zonation in arctic and alpine tundra and fellfield ecobioses. In Polunin, N. (ed.), *Ecosystem Theory Application*. London: Wiley, 35–62.
- Dai, X. Y., Ping, C. L., Candler, R., Haumaier, L., and Zech, W., 2001: Characterization of soil organic matter fractions of tundra soils in arctic Alaska by carbon-13 nuclear magnetic resonance spectroscopy. *Soil Science Society of America Journal*, 65: 87–93.
- Dai, X. Y., Ping, C. L., and Michaelson, G. J., 2002: Characterizing soil organic matter in Arctic tundra soil by different analytical approaches. *Organic Geochemistry*, 33: 407–419.
- Dalias, P., Anderson, M. J., Bottner, P., and Coûteaux, M. M., 2001: Long-term effects of temperature on carbon mineralization processes. *Soil Biology and Biochemistry*, 33: 1049–1057.
- Delaloye, R., and Reynard, E., 2001: Les éboulis gelés du Creux du Van (Chaîne du Jura, Suisse). In *Environnements périglaciaires, Notes et Comptes-Rendus du Groupe Régionalisation du Périglaciaire* No. XXVI, Association Française du Périglaciaire, 8: 118–129.
- Delaloye, R., Reynard, E., Lambiel, C., Marescot, L., and Monnet, R., 2003: Thermal anomaly in a cold scree slope (Creux du Van, Switzerland). *Permafrost: Proceedings of the Eighth International Conference on Permafrost*, 21–25 July 2003, Zurich, Switzerland, 175–180.
- Dorrepaa, E., Cornelissen, J. H. C., Aerts, R., Wallén, B., and van Logtestijn, R. S. P., 2005: Are growth forms consistent predictors of leaf litter quality and decomposability across peatlands along a latitudinal gradient? *Journal of Ecology*, 93: 817–828.
- Duchauffour, P., 1976: *Atlas écologique des sols du monde*. Paris: Masson.
- Duchauffour, P., 1983: *Pédologie I: Pédogénèse et classification*. Paris: Masson.
- Durand, B., and Monin, J. C., 1980: Elemental analysis of kerogens (C, H, O, N, S, Fe). In Durand, B. (ed.), *Kerogen: Insoluble Organic Matter from Sedimentary Rocks*. Paris: Editions Technip, 113–142.
- French, H. M., 1996: Permafrost. In French, H. M. (ed.), *The Periglacial Environment*. Edinburgh: Longman, 51–79.
- Freppaz, M., Rosso, F., Stockli, V., Phillips, M., Celi, L., and Zanini, E., 2008: A cold site located below the limit of discontinuous alpine permafrost: soil nutrient dynamics and plant characteristics. In Tian-Xiao Liu (ed.), *Soil Ecology Research Developments*. New York: Nova Publisher, 197–216. ISBN: 1-60021-971-3.
- Gaudinski, J. B., Trumbore, S. E., Davidson, E. A., and Zheng, S., 2000: Soil carbon cycling in a temperate forest: radiocarbon-based estimates of residence times, sequestration rates and partitioning of fluxes. *Biogeochemistry*, 51: 33–69.
- Gobat, J. M., Aragno, M., and Matthey, W., 2004: *The Living Soil: Fundamentals of Soil Science and Soil Biology*. Enfield, New Hampshire: Science Publishers, 626 pp.
- Grieve, I. C., 2000: Effects of human disturbance and cryoturbation on soil iron and organic matter distributions and on carbon storage at high elevations in the Cairngorm Mountains, Scotland. *Geoderma*, 95: 1–14.
- Haumaier, L., and Zech, W., 1995: Black carbon—Possible source of highly aromatic components of soil humic acids. *Organic Geochemistry*, 23: 191–196.
- Hobbie, S. E., Schimel, J. P., Trumbore, S. E., and Randerson, J. R., 2000: Controls over carbon storage and turnover in high-latitude soils. *Global Change Biology*, 6: 196–210.
- IUSS Working Group WRB, 2006: *World Reference Base for Soil Resources 2006*. 2nd edition. Rome: FAO, World Soil Resources Reports No. 103.
- Jenny, H., 1980: *The Soil Resource: Origin and Behaviour*. Ecological Studies 37. New York: Springer.
- Johnson, L. C., and Damman, W. H., 1991: Species controlled *Sphagnum* decay on a south Swedish raised bog. *Oikos*, 61: 234–242.
- Kneisel, C., Hauck, C., and Vonder Muhll, D., 2000: Permafrost below the timberline confirmed and characterized by geoelectrical resistivity measurements, Bever valley, eastern Swiss Alps. *Permafrost and Periglacial Processes*, 11: 295–304.
- Kögel-Knabner, I., 2002: The macromolecular organic composition of plant and microbial residues as inputs to soil organic matter. *Soil Biology and Biochemistry*, 34: 139–162.
- Kononova, M., 1966: *Soil Organic Matter*. London: Pergamon.
- Körner, C., 1989: The nutritional status of plants from high altitudes. A worldwide comparison. *Oecologia*, 81: 379–391.
- Körner, C., 1998: A re-assessment of high elevation treeline positions and their explanation. *Oecologia*, 115: 445–459.
- Körner, C., and Hoch, G., 2006: A test of treeline theory on a montane permafrost island. *Arctic, Antarctic, and Alpine Research*, 38: 113–119.
- Lang, S. I., Cornelissen, J. H. C., Klahn, T., van Logtestijn, R. S. P., Broekman, R., Schweikert, W., and Aerts, R., 2009: An experimental comparison of chemical traits and litter decomposition rates in a diverse range of subarctic bryophyte, lichen and vascular plant species. *Journal of Ecology*, 97: 886–900.
- Lesquereux, L., 1844: Quelques recherches sur les marais tourbeux en general. Neuchâtel, Switzerland: H. Wolfrath.
- Mikan, C. J., Schimel, J. P., and Doyle, A. P., 2002: Temperature controls of microbial respiration in arctic tundra soils above and below freezing. *Soil Biology and Biochemistry*, 34: 1785–1795.
- Nelson, D. W., and Sommers, L. E., 1982: Total carbon, organic carbon and organic matter. In Page, A. L. (ed.), *Methods of Soil Analysis. Part 2*. Madison, Wisconsin: American Society of Agronomy, 199 pp.
- Oleksyn, J., Modrzyński, J., Tjoelker, M. G., Zytowski, R., Reich, P. B., and Karolewski, P., 1998: Growth and physiology of *Picea abies* populations from elevational transects: common garden evidence for altitudinal ecotypes and cold adaptation. *Functional Ecology*, 4: 573–590.
- Orlov, D. S., Baranovskaja, V. A., and Okolelova, A. A., 1987: Organic matter of Povolje steppe soils and its transformation due to irrigation. *Pochvovedenie*, 10: 65–79.

- Painter, T. J., 1991: Lindow man, tollund man and other peat-bog bodies—The preservative and antimicrobial action of sphagnum, a reactive glycuronoglycan with tanning and sequestering properties. *Carbohydrate Polymers*, 15: 123–142.
- Paul, E. A., Follett, R. F., Leavitt, S. W., Halvorson, A., Peterson, G. A., and Lyon, D. J., 1997: Radiocarbon dating for determination of soil organic matter pool sizes and dynamics. *Soil Science Society of America Journal*, 61(4): 1058–1067.
- Ping, C. L., Michaelson, G. J., and Kimble, J. M., 1997: Carbon storage along a latitudinal transect in Alaska. *Nutrient Cycling in Agroecosystems*, 49: 235–242.
- Post, W. M., Emanuel, W. R., Zimke, P. J., and Stangenberger, A. G., 1982: Soil carbon pools and world life zones. *Nature*, 298: 156–159.
- Richard, J. L., 1961: *Les forêts acidophiles du Jura*. Berne: Hans Huber, 101 pp.
- Saiz-Jimenez, C., 1996: The chemical structure of humic substances: recent advances, In Piccolo, A. (ed.), *Humic Substances in Terrestrial Ecosystems*. Amsterdam: Elsevier Science, 1–44.
- Sarathchandra, S. U., Perrott, K. W., and Littler, R. A., 1989: Soil microbial biomass: influence of simulated temperature changes on size, activity and nutrient-content. *Soil Biology and Biochemistry*, 21: 987–993.
- Schmidt, I. K., Jonasson, S., and Michelsen, A., 1999: Mineralization and microbial immobilization of N and P in arctic soils in relation to season, temperature and nutrient amendment. *Applied Soil Ecology*, 11: 147–160.
- Schnitzer, M., 1982: Organic matter characterization. In Page, A. L. et al. (eds.), *Methods of Soil Analysis Part 2*. Second Edition. Agronomy 9. Madison, Wisconsin: American Society of Agronomy and Soil Science Society of America.
- Shaver, G. R., Giblin, A. E., Nadelhoffer, K. J., Thieler, K. K., Downs, M. R., Laundre, J. A., and Rastetter, E. B., 2006: Carbon turnover in Alaskan tundra soils: effects of organic matter quality, temperature, moisture and fertilizer. *Journal of Ecology*, 94(4): 740–753.
- Skoog, D., and West, D., 1987: *Analytical Chemistry: an Introduction*. 2nd Italian edition. Philadelphia: W. B. Saunders Co., 751 pp.
- Soil Survey Staff, 2003: *Soil Taxonomy. A Basic System of Soil Classification for Making and Interpreting Soil Surveys*. 2nd edition. Washington, D.C.: U.S. Government Printing Office, U.S. Department of Agriculture & Natural Resources Conservation Service, Agriculture Handbook Number 436.
- Spaccini, R., Piccolo, A., Conte, P., Haberhauer, G., and Gerzabek, M. H., 2002: Increased soil organic carbon sequestration through hydrophobic protection by humic substances. *Soil Biology and Biochemistry*, 34: 1839–1851.
- Stevenson, F. J., 1994: *Humus Chemistry: Genesis, Composition and Reactions*. New York: John Wiley & Sons.
- Stuiver, M., and Polach, H. A., 1977: Reporting of ^{14}C data. *Radiocarbon*, 19: 355–363.
- Trumbore, S. E., Chadwick, O. A., and Amundson, R., 1996: Rapid exchange of soil carbon and atmospheric CO_2 driven by temperature change. *Science*, 272: 393–396.
- Tschager, A., Hilscher, H., Franz, S., Kull, U., and Larcher, W., 1982: Jahreszeitliche Dynamik der Fettspeicherung von *Loiseleuria procumbens* und anderen Ericaceen der alpinen Zwergstrauchheide. *Acta Oecologica-Oecologia Plantarum*, 3: 119–134.
- Uhlířová, E., Santruckova, H., and Davidov, S. P., 2007: Quality and potential biodegradability of soil organic matter preserved in permafrost of Siberian tussock tundra. *Soil Biology and Biochemistry*, 39: 1978–1989.
- Webster, R., 2001: Statistics to support soil research and their presentation. *European Journal of Soil Science*, 52: 331–340.
- Weih, M., and Karlsson, P. S., 2001: Growth response of mountain birch to air and soil temperature: Is increasing leaf-nitrogen content an acclimation to lower air temperature? *New Phytologist*, 150: 147–155.
- Weintraub, M. N., and Schimel, J. P., 2003: Interactions between carbon and nitrogen mineralization and soil organic matter chemistry in arctic tundra soils. *Ecosystems*, 6: 87–93.
- Williams, B. L., and Sparling, G. P., 1988: Microbial biomass carbon and readily mineralized nitrogen in peat and forest humus. *Soil Biology and Biochemistry*, 20: 579–581.
- Williams, B. L., Shand, C. A., Hill, M., O'Hara, C., Smith, S., and Young, M. E., 1995: A procedure for the simultaneous oxidation of total soluble nitrogen and phosphorus in extracts of fresh and fumigated soils and litters. *Communication Soil Science Plant Analysis*, 26: 91–106.
- Zang, X., van Heemst, J. D. H., Dria, K. J., and Hatcher, P. G., 2000: Encapsulation of protein in humic acid from a histosol as an explanation for the occurrence of organic nitrogen in soil and sediment. *Organic Geochemistry*, 31: 679–695.
- Ziegler, F., and Zech, W., 1989: Distribution pattern of total lipids and lipids fractions in forest humus. *Zeitschrift für Pflanzenernährung und Bodenkunde*, 152: 287–290.

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