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SYNTHESIS AND EMERGING IDEAS

Decomposition of soil organic matter from boreal black spruce forest: environmental and chemical controls

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Abstract Black spruce forests are a dominant covertype in the boreal forest region, and they inhabit landscapes that span a wide range of hydrologic and thermal conditions. These forests often have large stores of soil organic carbon. Recent increases in temperature at northern latitudes may be stimulating decomposition rates of this soil carbon. It is unclear, however, how changes in environmental conditions influence decomposition in these systems, and if substrate controls of decomposition vary with hydrologic and thermal regime. We addressed these issues by investigating the effects of temperature, moisture, and organic matter chemical characteristics on decomposition of fibric soil horizons from three black spruce forest sites. The sites varied in drainage and permafrost, and included a "Well Drained" site where permafrost was absent, and "Moderately well Drained" and "Poorly Drained" sites where permafrost was present at about 0.5 m depth. Samples collected from each site were incubated at five different moisture contents (2, 25, 50, 75, and 100% saturation) and two different temperatures (10°C and 20°C) in a full factorial design for two months. Organic matter chemistry was analyzed using pyrolysis gas chromatography-mass spectrometry prior to incubation, and after incubation on soils held at 20°C, 50% saturation. Mean cumulative mineralization, normalized to initial carbon content, ranged from 0.2% to 4.7%, and was dependent on temperature, moisture, and site. The effect of temperature on mineralization was significantly influenced by moisture content, as mineralization was greatest at 20°C and 50–75% saturation. While the relative effects of temperature and moisture were similar for all soils, mineralization rates were significantly greater for samples from the "Well Drained" site compared to the other sites. Variations in the relative abundances of polysaccharide-derivatives and compounds of undetermined source (such as toluene, phenol, 4-methyl phenol, and several unidentifiable compounds) could account for approximately 44% of the variation in mineralization across all sites under ideal temperature and moisture conditions. Based on our results, changes in temperature and moisture likely have similar, additive effects on in situ soil organic matter (SOM) decomposition across a wide range of black spruce forest systems, while variations in SOM chemistry can lead to significant differences in decomposition rates within and among forest sites.

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Introduction

Boreal soils have been accumulating carbon (C) since the retreat of the Laurentide ice sheet, roughly 10,000 years ago (Harden et al. 1992), and these soils currently contain about one-third of the world's soil organic carbon (Billings 1987; Post et al. 1982; Gorham 1991). The recent rise in air temperatures at northern latitudes may be accelerating soil organic matter decomposition in boreal regions (Oechel et al. 1993; Goulden et al. 1998; Serreze et al. 2000). A net release of C stored in boreal soils due to increasing temperatures could have a significant positive feedback on global warming by increasing atmospheric CO_2 and CH_4 (McGuire et al. 2000; Keyser et al. 2000). The positive effect of temperature on soil organic C decomposition is well-studied in many ecosystems (Trumbore et al. 1996; Katterer et al. 1998; Dalias et al. 2001; Knorr et al. 2005). However, there is some debate as to whether warmer temperatures will cause a sustained increase in soil C decomposition (Liski et al. 1999; Giardini and Ryan 2000; Jarvis and Linder 2000; Grace and Rayment 2000). Environmental constraints, including drought, flooding, freezing temperatures, and physical and chemical protection of soil organic C, can limit temperature sensitivity of soil organic matter decomposition (Davidson and Janssens 2006).

The primary controls of decomposition include temperature (Van Cleve and Dyrness 1983; Hobbie 1996; Christensen et al. 1999; Neff and Hooper 2002), moisture (Ponnamperuma 1972; Gulledge and Schimel 1998; Schimel et al. 1999), and substrate quality (Flanagan and Van Cleve 1983; Hobbie et al. 2000). Substrate quality, as indicated by carbon chemistry and nutrient content, can be of equal or greater importance than temperature as a control on decomposition (Flanagan and Van Cleve 1983; Nadelhoffer et al. 1991; Hobbie et al. 2000). The interactions between temperature, moisture, and substrate quality, and their effects on decomposition in boreal ecosystems, are particularly complex (Bonan and Shugart 1989; Chapin et al. 2000; Carrasco et al. 2006). For example, the distribution of permafrost in boreal regions is dependent chiefly on soil temperature, but also secondarily on soil water content and the presence of insulating moss and organic soil layers (Bonan and Shugart 1989). Vegetation found on cold wet permafrost soils, such as coniferous trees and mosses, deposit litter that is generally characterized as being resistant to decomposition due to low substrate quality (Moore 1984; Hobbie 1996). These interrelations give rise to the question of the relative importance of these individual factors to decomposition of boreal soil C and litter, and they complicate the prediction of the effects of climate change on decomposition in boreal systems.

In an effort to understand how temperature, moisture, and substrate quality interact to influence decomposition in boreal systems, we conducted a study focusing on decomposition of soil organic matter (SOM) from Alaska black spruce ((*Picea mariana* Mill.) B.S.P.) forest varying in permafrost extent, drainage, and groundcover vegetation. Black spruce is the principal vegetation type within the boreal forest biome of North America (Van Cleve and Dyrness 1983; Hall et al. 1997), and it occupies sites spanning a range of permafrost and drainage conditions. Poorly drained lowlands with shallow permafrost typically have thick *Sphagnum* moss cover and substantial organic soil accumulation, while better drained uplands have deep or absent permafrost, groundcover vegetation dominated by feathermosses, and less organic soil accumulation (Harden et al. 1997; Bisbee et al. 2001). The objectives of the study described in this paper were to: (1) determine whether SOM formed from varying source material, and maintained under different environmental conditions, have inherently different decomposition potentials under the same conditions; (2) characterize the independent and combined influences of temperature and moisture on SOM decomposition; and (3) examine differences in black spruce forest SOM chemical characteristics and determine its importance to decomposition.

Methods

Site description and soil collection

The three study sites are located in central Alaska (Fig. 1) in areas underlain by discontinuous permafrost. The sites are black spruce forest systems that

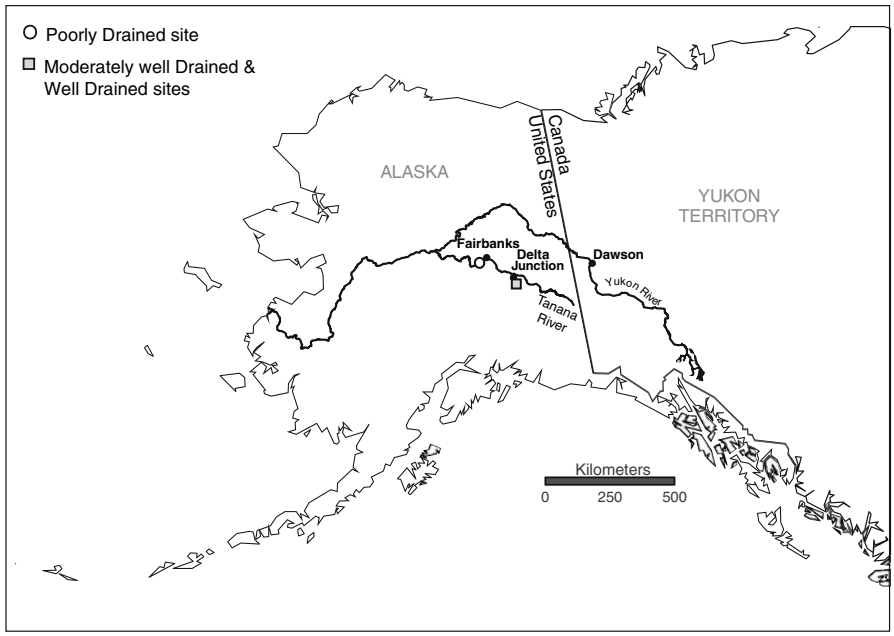

Fig. 1 Map of study site locations

vary in drainage, permafrost depths, organic layer thickness, stand density, and dominant groundcover vegetation (Table 1). A "Well Drained" site (inceptisol cryept) and a "Moderately well Drained" site (gelisol orthel) are located in mature black spruce forest (80–100 years old) near Delta Junction, AK (63°53′ N, 145°44′ W) (Manies et al. 2004). Soils in this area are mainly derived from Donnelly moraine and wind-blown loess (O'Neill 2000), and are underlain by deposits of sand and gravel. In early spring, water collects in the surface soils on top of the seasonal ice layer. Water drains into deeper soils and then disappears by early June at the "Well Drained" site as the seasonal ice layer melts, but the presence of permafrost prevents the water from completely draining at the "Moderately well Drained" site. A "Poorly Drained" site (gelisol histel) is located in a mature black spruce stand (up to 130 years old) on the Tanana River floodplain near Fairbanks, AK (64°42′ N, 148°19′ W). Permafrost and underlying alluvial material prevent vertical movement of water, so the water table is within 35–40 cm of the surface during the entire snow-free season.

Soil samples were collected from each site at five locations along sampling transects ranging from 40–120 m in length. The location of the sampling transects at the "Well Drained" and "Moderately well Drained" sites are described in detail by Manies et al. (2004), and the sampling transect at the "Poorly Drained" site is described by Wickland et al. (2006). Blocks of soil were collected from various depths at each transect location based on the depth of the fibric organic horizon (analogous to Oi horizon), which is characterized by an accumulation of partly decomposed organic matter often having some recognizable plant structures (Canadian System of Soil Classification 1998). The depths of the fibric layer were highly spatially heterogeneous within sites, but typically extended from 2–10 cm depth at "Well Drained", 5–15 cm depth at "Moderately well Drained", and 5–30 cm depth at "Poorly Drained" (Manies et al. 2004; Manies and Wickland, unpublished data). We analyzed and incubated fibric soil horizons from each site so that we could make a direct comparison of SOM that were at a similar stage in decomposition. The intact soil blocks were placed in Ziploc bags, put in coolers on ice, and transported to Fairbanks, AK where the soils were then frozen. The soils remained frozen during transport to Boulder, CO.

Soil sample preparation and analyses

The soils were thawed in the laboratory and trimmed so that only fibric soil horizon remained. Roots >2 mm in thickness were removed and the soils were homogenized by hand. Subsamples were removed from each soil sample for organic matter (OM)

Table 1 Site characteristics

Site	Permafrost depth (cm)	Mean O layer thickness (cm)	Stand density (trees ha^{-1})	Moss cover (%)	Dominant moss species, %	Lichen cover (%)	Other vegetation
Well Drained	no permafrost	10.5	7053[a]	64	*Hylocomium* sp, 91%	28	*Arctostaphylos* sp., *Ledum* sp., *Vaccinium* sp., *scattered Betula papyrifera*
Moderately well Drained	43 (range:37–55)	20	5505[b]	87	*Hylocomium* sp, 54% *Aulacomium* sp., 22%	10	*Arctostaphylos* sp., *Ledum* sp., *Vaccinium* sp.
Poorly Drained	41 (range: 36–43)	90	2626	~90	*Sphagnum* sp., ~40% *Hylocomium* sp., ~40% *Pleurozium* sp., ~20%	~2	*Eriophorum* sp., *Betula nana*, *Ledum* sp., *Vaccinium* sp.

Moss cover, lichen cover, and O layer thickness for WD and MD are from Manies et al. 2001

[a] Manies et al. (2004)

[b] Harden and Manies, unpublished data

content, carbon and nitrogen (C and N) content, and pyrolysis-gas chromatography/mass spectrometry (py-GC/MS) analysis. The subsamples were dried at 60°C for 24 h and ground prior to analyses. Organic matter content (% w/w) was determined by combusting the soils at 550°C for 18 h and measuring the change in mass, and soil particle density was calculated assuming the densities of OM and mineral matter are 1.0 and 2.65 g cm^{-3}, respectively (Skopp 2000). C and N content (w/w) were measured on three replicates per sample using a CE-440 Elemental Analyzer (Exeter Analytical, Inc).

Pyrolysis-gas chromatography/mass spectrometry analyses

To describe differences in OM chemical characteristics among sites, and the changes that occurred during decomposition, we analyzed soil samples before and after incubation using py-GC/MS. This method thermally degrades complex organic matter into smaller molecular units, which are then separated and analyzed by gas chromatography and mass spectrometry. Py-GC/MS provides a "fingerprint" of organic matter constituents, and provides relative abundances of different compounds rather than absolute quantities. Saiz-Jimenez (1994a) presents an overview of the advantages and the limitations of this analytical technique. We analyzed five samples from each site prior to incubation. In addition, five post-incubation samples from each site at one incubation condition (20°C, 50% saturation) were analyzed to determine which compounds were most altered during the incubation. Samples were pyrolyzed for 10 s in a GSG Analytical Pyromat Curie-Point pyrolyzer, using a ferromagnetic tube with a Curie-point of 590°C. The pyrolysis products were sent directly to a Trace GC gas chromatograph with He carrier gas (flow rate = 1.0 mL/min), with an interface temperature of 250°C and a split injection (split ratio 50:1). The pyrolysis products were separated on a BPX 5 column (60 m × 0.25 mm, film thickness = 0.25 μm), using a temperature program of 35°C for 5 min, 5°C min^{-1} increase to 270°C, followed by 30°C min^{-1} increase to 300°C. The column outlet was coupled to a Thermo Polaris-Q ion-trap mass spectrometer run at 70 eV in the EI mode. The transfer line was held at 270°C, and the source temperature was 200°C.

The pyrolysis products were identified by comparing results to reference spectra after deconvolution and extraction using AMDIS v 2.64 software (http://www.amdis.net) and National Institute of Standards and Technology (NIST) mass spectral libraries (NIST Standard Reference Database Number 69, June 2005 Release, http://www.webbook.nist.gov/chemistry/) and published literature. Relative compound abundances were calculated by normalizing peak intensity of each compound to the sum of the peak intensities for the sample. We grouped individual compounds by probable source into the following classes: lignin, lipid, polysaccharide, and nitrogen compounds (Saiz-Jimenez and de Leeuw 1984a, b; Saiz-Jimenez 1994b; Stankiewicz et al. 1997; Nierop et al. 2001; de Alcântara et al. 2004; Buurman et al. 2005). Compounds whose source origin is unknown or ambiguous, and unidentifiable compounds were categorized as "undetermined".

Incubation

The incubation was designed to test the influence of temperature, moisture content, and the combined influences of temperature and moisture on OM decomposition from the three sites. We incubated the soil samples at five different moisture contents (2, 25, 50, 75, and 100% saturation) and two different temperatures (10 and 20°C) in a full factorial design. Prior to incubation, the homogenized samples were dried at 40°C for 2 days to bring the samples to minimum moisture content. The dried samples from each sample location (total of 15 sample locations, five locations per site) were then divided into ten 1–6 g portions and placed in pre-combusted 120 mL glass jars. Large soil clods (>5 mm) were broken up once the soils were in the jars. The samples were brought to the appropriate moisture content one day before the incubation began. Two replicates from each sample location were designated as "100% saturation", and measured amounts of deionized water were added to each sample until they were saturated (water could no longer be absorbed). The saturated soils were weighed, and the amount of water added per gram dry mass was determined for each soil. The amounts of water needed to bring the remaining samples to 2, 25, 50, and 75% saturation were calculated by linear interpolation based on the individual dry weights and the amount of water needed to bring the soils to 100% saturation. The jars were sealed with lids and placed in incubators set at 10°C or 20°C. The jars were weighed weekly after respiration measurements to determine evaporative water loss and, when necessary, water was added to bring the soil samples to their initial weight.

Soil respiration rates were measured on days 0, 2, 4, 7, and once weekly thereafter to day 57 (no measurements were made between days 42 and 57). Prior to respiration measurements, the jar lids were removed for about 20 min to allow headspace equilibration with the atmosphere. Soil respiration was measured by placing an open soil jar into a 0.5 L Mason jar which was partially filled with clean glass marbles to reduce headspace volume. The Mason jar lids were fitted with a sampling port consisting of a Swagelok fitting and a removable septum. The Mason jar was sealed and the headspace was immediately sampled using a 0.5 mL glass syringe fitted with a needle. The sample was analyzed for CO_2 concentration using a Licor 6252 infrared CO_2 analyzer having nitrogen carrier gas. The headspace was sampled and analyzed four times, and the mean CO_2 concentration was calculated (calibration curves were determined using four standards). The jars were returned to the appropriate incubator until headspace CO_2 concentration was measured again about 2 hours later. Soil respiration rate was calculated as the change in headspace CO_2 concentration (adjusted for headspace volume and ambient temperature and pressure) and dissolved CO_2 concentration with time, assuming a linear change in CO_2 concentration. The change in dissolved CO_2 concentration was calculated from headspace concentrations, soil water contents, and known CO_2 equilibrium constants (Plummer and Busenberg 1982) adjusted for ambient temperature and pressure (Striegl et al. 2001). Cumulative soil respiration for the entire incubation was calculated for each soil sample by linear interpolation between sequential respiration measurements.

Decomposition constant calculations

Decomposition constants for each site at the five moisture conditions and two temperatures were determined using the average time series of initial %C mineralized for each temperature-moisture

condition of the corresponding five replicates. We fitted a single exponential model (Eq. 1) to the incubation results assuming one C pool:

$$\text{Mineralized C (\% initial C)} = 100*(1 - e^{-kt}) \quad (1)$$

where t = time (days) and k = decomposition rate constant (day^{-1}). We also fitted a two-pool model (Eq. 2) to the incubation results (Kalbitz et al. 2003):

$$\text{Mineralized C (\% initial C)} = (100 - a)*(1 - e^{-k2t}) + a*(1 - e^{-k1t}) \quad (2)$$

where t = time (days), $k1$ = decomposition rate constant of "stable" C (slowly mineralizable C pool, yr^{-1}), a = the relative size of the stable C pool (%), $k2$ = decomposition rate constant of "labile" C (rapidly mineralizable C pool, day^{-1}). The curves were fitted using a least-squares regression (Levenberg-Marquardt method). We report single pool decomposition constants for all incubations, and two-pool model decomposition constants for incubations where the two-pool model $R^2 \geq$ one-pool model R^2. We calculated mean residence time (MRT) of the pools from the corresponding k values as:

$$\text{MRT} = (1/k)/365 \quad (3)$$

where k is in d^{-1} and MRT is in yr^{-1}.

Statistics

We used analysis of variance (ANOVA) and post-hoc tests (Tukey's HSD test), at $\alpha = 0.05$ significance level, to test for differences in general SOM chemical properties (C and N content, C:N, %OM, particle density), for within-site differences in cumulative mineralization, and for the effects of temperature, moisture, and site (individual and interactive effects) on cumulative mineralization. We tested for between-site differences in py-GC/MS results using repeated measures ANOVA and post-hoc tests (Fisher LSD test). We used principal components analysis (PCA) to condense py-GC/MS results into a smaller number of variables, or factors, which could be used to describe differences in SOM chemical characteristics. Simple linear regressions were used to test the significance of correlation between several pairs of variables. Curve-fitting by least-squares regression was used for decomposition rates and decomposition–moisture relations. We used Statistica 7.1 (StatSoft, Inc.) for all statistical analyses.

Results

Soil organic matter chemistry

Conventional descriptions of SOM quality, such as C and N content and ratios, were not significantly different across the three study sites (Table 2). There was a general trend, however, for soil samples from "Poorly Drained" to have greater C, N, and OM content than samples from "Moderately well Drained" and "Well Drained". Despite these similarities, there were broad differences in more detailed structural indicators of SOM quality among sites. Pyrolysis-GC/MS results, expressed as relative amounts of compound sources (Table 3), demonstrate a significant difference among sites (ANOVA, $F = 4.9*10^4$, $p < 0.00$). Polysaccharide-derived compounds were significantly lower in "Poorly Drained" samples than "Moderately well Drained" and "Well Drained" samples (Fisher LSD test, $p = 0.05$ and 0.06, respectively), while lipid-derived compounds were significantly lower in "Well Drained" than in

Table 2 General physical and chemical soil organic matter properties, and water:soil ratio for 100% saturation incubation

Site	C content ($g\ kg^{-1}$)	N content ($g\ kg^{-1}$)	C:N ratio	% Organic matter	Particle density ($g\ cm^{-3}$)[a]	100% saturation g H_2O/g dry soil
Well Drained	31.0 (4.9)	1.16 (0.1)	26.3 (1.2)	62.7 (9.3)	1.33 (0.11)	2.97 (0.51)
Moderately well Drained	29.6 (1.1)	1.18 (0.05)	25.1 (1.0)	60.5 (1.9)	1.33 (0.02)	2.66 (0.09)
Poorly Drained	34.7 (0.9)	1.58 (0.14)	22.7 (2.2)	71.7 (2.2)	1.22 (0.02)	3.58 (0.22)

C content, N content, and C:N ratios are the means and SE of 15 subsamples

% Organic Matter, Particle densities, and water:soil ratios are the means and SE of 5 subsamples

[a] Particle densities were calculated assuming organic and mineral soil densities of 1.0 and 2.65 g cm^{-3}, respectively

Table 3 Relative percent of compound source classes in soil samples determined by pyrolysis GC/MS analyses, pre- and post-incubation[a]

Site	Lignin (%)	Lipids (%)	Polysaccharides (%)	N-compounds (%)	Undetermined (%)
Well Drained					
Pre-incubation	32.6 (6.1)	0.7 (0.1)	27.6 (4.3)	5.3 (0.5)	33.7 (4.3)
Post-incubation	38.2 (7.2)	1.2 (0.8)	21.7 (4.7)	2.9 (1.4)	36.0 (3.6)
Moderately well Drained					
Pre-incubation	23.8 (2.5)	3.8 (1.0)	28.0 (0.7)	5.5 (0.6)	38.9 (2.3)
Post-incubation	38.1 (6.3)	3.4 (1.8)	17.3 (3.4)	2.5 (0.8)	38.8 (4.0)
Poorly Drained					
Pre-incubation	31.7 (2.6)	2.8 (1.4)	20.1 (1.1)	6.5 (1.3)	38.9 (2.3)
Post-incubation	28.7 (6.3)	4.6 (1.4)	22.1 (4.0)	3.9 (0.8)	40.7 (4.7)

[a] Each value is the mean (SE) of five samples

"Moderately well Drained" samples ($p = 0.05$). Within the "undetermined" compound class, 32.6% (SE = 1.5) and 22.4% (SE = 1.3) of the relative abundances were to attributable aromatic and phenolic compounds. Unidentifiable compounds accounted for most of the remaining proportion.

Principal components analysis identified two factors that together accounted for 96.1% of the variance in OM chemistry (Fig. 2). Factor 1 was highly correlated to the relative amounts of lignin-derived, polysaccharide-derived, and "undetermined" compounds (correlation coefficient, $r = 0.99$, -0.75, and -0.66 respectively), while factor 2 was correlated with relative amounts of polysaccharide-derived ($r = -0.66$), "undetermined" ($r = 0.74$), and lipid-derived compounds ($r = 0.73$). The contributions of the variables to factor 1 were lignin: 0.71, polysaccharides: 0.19, and "undetermined": 0.09; the contributions to factor 2 were polysaccharides: 0.52, "undetermined": 0.37, and lipids: 0.09. Relative abundances of nitrogen compounds were not important for either factor. The samples clustered in fairly distinct groups according to site, indicating consistent relative differences in multiple compound source classes among the samples within each site (Fig. 2).

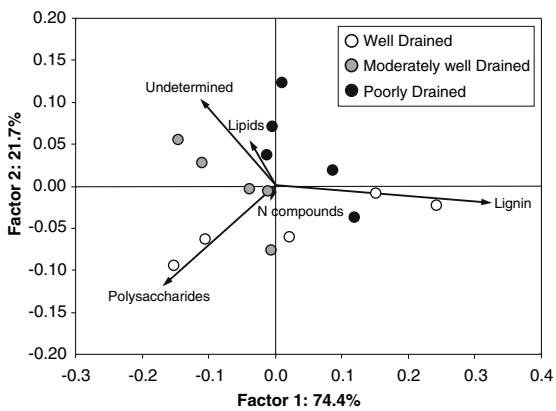

Fig. 2 Principal components analysis of pyrolysis GC/MS results, by compound source, of soil samples before incubation. Each point represents one sample

There were several dominant compounds in each source class which were common to all the sites (Table 4; Appendix 1 lists all identified compounds). Vinylguaiacol was the most abundant lignin-derived compound at all sites and furfural was the dominant polysaccharide-derived compound, although it was notably reduced in samples from "Poorly Drained". Toluene, phenol, and 4-methyl phenol were the most abundant compounds of "undetermined" source.

Effects of temperature, moisture, and site on decomposition

Soil respiration exhibited similar temporal patterns, and similar responses to temperature and moisture, across all sites (Fig. 3). Respiration peaked within the first four days then dropped quickly to relatively low rates through the rest of the incubation. There was a significant difference in total % of initial C mineralized between individual samples from "Poorly Drained" (ANOVA, $F = 9.35$, $p < 0.0001$), but we chose to keep these samples as a single group for statistical comparisons between sites. Total % of initial C mineralized did not vary significantly among samples within the "Well Drained" or "Moderately well Drained" sites.

Table 4 Dominant compounds and mean (SE) relative percent for lignin, polysaccharide, and undetermined compound classes

Compound	Source	Well Drained (%)	Moderately well Drained (%)	Poorly Drained (%)
Vinylguaiacol (Phenol, 2-methoxy-4-vinyl-)	Lignin	9.6 (1.3)	7.6 (0.4)	10.2 (1.1)
Methylguaiacol (Phenol, 2-methoxy-4-methyl-)	Lignin	5.6 (1.2)	3.8 (0.5)	3.6 (0.4)
Isoeugenol (Phenol, 2-methoxy-4-propenyl-)	Lignin	4.9 (0.9)	3.6 (0.5)	3.7 (0.6)
Guaiacol (Phenol, 2-methoxy)	Lignin	4.4 (1.5)	3.6 (1.0)	3.8 (0.3)
Furfural	Polysaccharide	9.0 (1.3)	9.1 (0.5)	6.4 (0.5)
Furan, 3-methyl	Polysaccharide	2.2 (0.2)	2.4 (0.1)	1.6 (0.1)
Levoglucosenone	Polysaccharide	3.1 (0.9)	4.2 (0.3)	2.0 (0.2)
2(5H)-Furanone	Polysaccharide	1.9 (0.3)	2.1 (0.1)	1.4 (0.1)
Toluene	Undetermined	3.3 (0.3)	4.4 (0.5)	3.8 (0.5)
Phenol	Undetermined	3.4 (0.5)	3.1 (0.4)	3.4 (0.5)
Phenol, 4-methyl-	Undetermined	3.5 (0.3)	2.7 (0.8)	3.7 (0.4)

Each value is the mean and SE of five samples

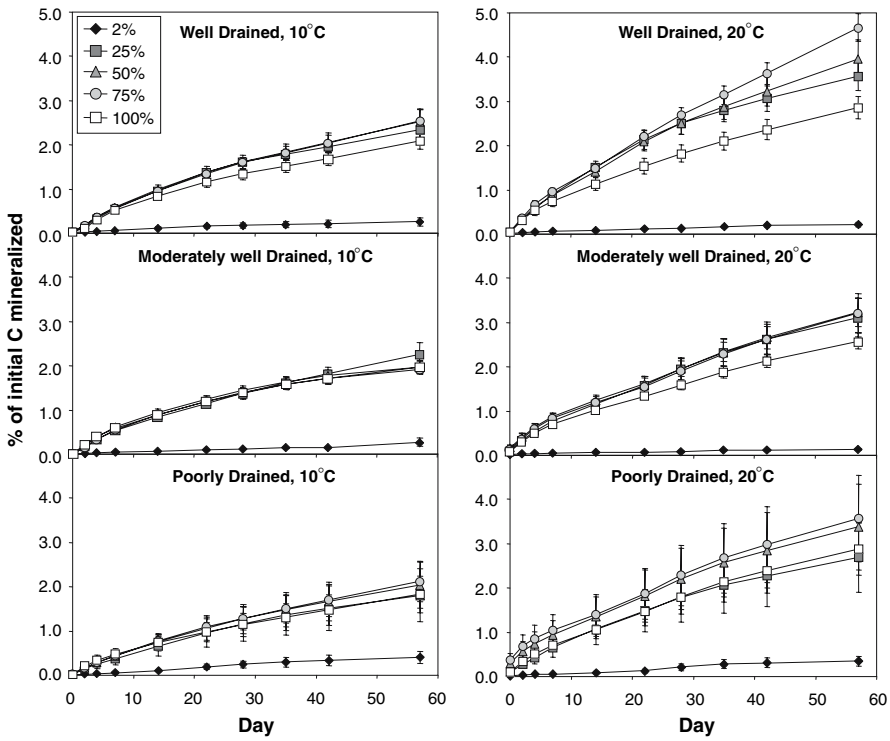

Fig. 3 Percent of initial soil C mineralized during incubation at 10°C and 20°C of Well Drained, Moderately well Drained, and Poorly Drained soils, as labeled in individual panels. Each point is the mean ± SE of five replicates. The different symbols correspond to five different moisture contents

Cumulative soil respiration was dependent on temperature, moisture, and site (factorial ANOVA, df = 2, n = 120; Table 5). Greater decomposition occurred at 20°C than at 10°C (F = 37.9, $p < 0.001$), and decomposition was significantly inhibited at 2% saturation (F = 43.1, $p < 0.001$; Tukey's HSD Test, $p < 0.001$). Soil samples from "Well Drained" had greater mineralization totals, normalized to initial C, than "Moderately well Drained" and "Poorly Drained" soils (F = 3.36, p = 0.038; Tukey's HSD Test, $p < 0.09$). Mean Q_{10} values ranged from 0.7 to 1.9 across all sites and moisture conditions (Table 5). We fitted quadratic equations to mean total mineralization of all sites versus moisture condition for 10°C

Table 5 Soil incubation results and decomposition constants

Site	Temperature (°C)	Moisture (%saturation)	% Initial C mineralized (SE)	Q_{10} (SE)	Single pool k (d^{-1})	Single pool MRT (yr)	Single pool R^2	Two pool % Labile C	Two pool % Stable C	Two pool Labile k_1 (d^{-1})	Two pool Stable k_2 (d^{-1})	Two pool Labile C MRT (d)	Two pool Stable C MRT (yr)	Two pool R^2
WD	10	2	0.26 (0.09)		5.40E−05	51	0.85	0.1	99.9	7.44E–02	2.00E–05	13	137	0.99
WD	10	25	2.33 (0.17)		4.85E–04	5.6	0.92	–	–	–	–	–	–	–
WD	10	50	2.52 (0.28)		5.07E–04	5.4	0.94	1.2	98.8	4.91E–02	2.40E–04	20	11	0.99
WD	10	75	2.55 (0.24)		5.05E–04	5.4	0.95	1.0	99.0	5.10E–02	2.80E–04	20	10	0.99
WD	10	100	2.09 (0.18)		4.19E–04	6.5	0.93	0.9	99.1	5.35E–02	2.10E–04	19	13	0.99
WD	20	2	0.22 (0.05)	1.4 (0.5)	4.50E–05	61	0.88	0.03	99.97	6.39E–01	3.00E–05	2	91	0.99
WD	20	25	3.57 (0.33)	1.5 (0.1)	7.57E–04	3.6	0.91	–	–	–	–	–	–	–
WD	20	50	3.96 (0.43)	1.6 (0.1)	7.96E–04	3.4	0.95	2.0	98.0	4.11E–02	3.80E–04	24	7.2	0.99
WD	20	75	4.67 (0.32)	1.9 (0.1)	8.97E–04	3.1	0.98	0.6	99.4	1.04E–01	7.20E–04	10	3.8	0.99
WD	20	100	2.86 (0.26)	1.4 (0.1)	5.81E–04	4.7	0.92	0.8	99.2	9.35E–02	3.60E–04	11	7.6	0.99
MD	10	2	0.28 (0.09)		4.40E–05	62	0.97	–	–	–	–	–	–	–
MD	10	25	2.26 (0.27)		4.45E–04	6.2	0.95	–	–	–	–	–	–	–
MD	10	50	1.97 (0.13)		4.31E–04	6.4	0.85	–	–	–	–	–	–	–
MD	10	75	1.93 (0.12)		4.16E–04	6.6	0.87	–	–	–	–	–	–	–
MD	10	100	1.97 (0.16)		4.21E–04	6.5	0.87	1.3	98.7	5.24E–02	1.30E–04	19	21	0.99
MD	20	2	0.13 (0.02)	0.7 (0.2)	2.90E–05	94	0.70	–	–	–	–	–	–	–
MD	20	25	3.11 (0.44)	1.4 (0.1)	6.30E–04	4.3	0.94	1.0	99.0	7.13E–02	3.90E–04	14	7.0	0.99
MD	20	50	3.23 (0.32)	1.6 (0.1)	6.47E–04	4.2	0.92	0.6	99.4	2.09E–01	4.70E–04	5	5.8	0.99
MD	20	75	3.22 (0.44)	1.7 (0.2)	6.35E–04	4.3	0.93	0.5	99.5	2.21E–01	4.80E–04	5	5.7	0.99
MD	20	100	2.58 (0.18)	1.3 (0.1)	5.19E–04	5.3	0.92	0.6	99.4	1.45E–01	3.60E–04	7	7.6	0.99
PD	10	2	0.41 (0.14)		7.80E–05	35	0.98	–	–	–	–	–	–	–
PD	10	25	1.81 (0.59)		3.65E–04	7.5	0.95	–	–	–	–	–	–	–
PD	10	50	2.04 (0.52)		4.05E–04	6.8	0.95	1.2	98.8	3.66E–02	1.80E–04	27	15	0.99
PD	10	75	2.12 (0.45)		4.16E–04	6.6	0.96	0.7	99.3	5.18E–02	2.50E–04	19	11	0.99
PD	10	100	1.83 (0.41)		3.65E–04	7.5	0.92	0.5	99.5	1.08E–01	2.30E–04	9	12	0.99
PD	20	2	0.35 (0.11)	0.9 (0.2)	6.90E–05	40	0.96	–	–	–	–	–	–	–
PD	20	25	2.69 (0.79)	1.6 (0.1)	5.56E–04	4.9	0.92	2.0	98.0	3.66E–02	1.60E–04	27	17	0.99
PD	20	50	3.38 (0.97)	1.6 (0.1)	6.98E–04	3.9	0.87	0.8	99.2	2.26E–01	4.80E–04	4	5.7	0.99
PD	20	75	3.57 (0.98)	1.6 (0.1)	7.32E–04	3.7	0.84	0.7	99.3	5.31E–01	5.30E–04	2	5.2	0.99
PD	20	100	2.88 (0.59)	1.7 (0.1)	5.81E–04	4.7	0.93	0.8	99.2	8.91E–02	3.80E–04	11	7.2	0.99

WD = "Well Drained", MD = "Moderately well Drained", PD = "Poorly Drained"

–, not applicable

MRT, Mean Residence Time

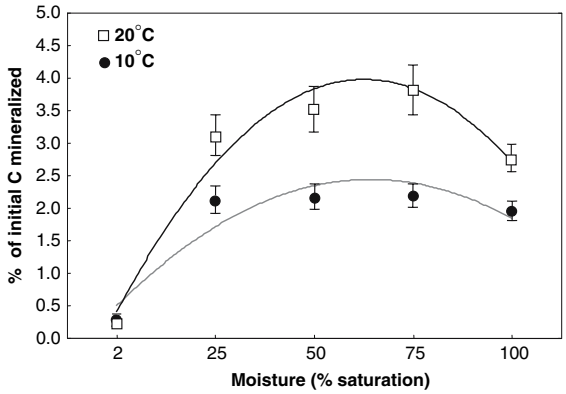

Fig. 4 Mean % of initial C mineralized versus soil moisture content at 10°C and 20°C. Each point is the mean ± SE of 15 samples (five samples each from Well Drained, Moderately well Drained, and Poorly Drained). The solid regression lines are the quadratic equations for each temperature: (10°C) $y = -0.30x^2 + 2.1x - 1.2$, $R^2 = 0.87$; (20°C) $y = -0.57x^2 + 4.1x - 3.3$, $R^2 = 0.95$

and 20°C (Fig. 4), as there was no significant site by moisture interaction. The resulting equations for 10°C and 20°C, respectively, are:

$$\%\ \text{of initial C mineralized} = -0.30*(\%\ \text{saturation})^2 + 2.1*(\%\ \text{saturation}) - 1.2 \quad (4)$$

$$\%\ \text{of initial C mineralized} = -0.57*(\%\ \text{saturation})^2 + 4.1*(\%\ \text{saturation}) - 3.3 \quad (5)$$

The coefficients in Eqs. 4 and 5 vary by a factor approximately equal to the maximum Q_{10} that was measured. There was a significant temperature by moisture interaction which varied with moisture ($F = 3.64$, $p < 0.01$, Fig. 4). Temperature had a significant positive effect on SOM decomposition at 50% and 75% saturation (Tukey's HSD Test, $p < 0.01$), but not at 2%, 25%, or 100% saturation.

Although the incubated SOM samples were altered by removing roots and disturbing the soil structure, we can make general comparisons between incubation and in situ soil moisture conditions to apply laboratory results to the field. During May-October 2003, surface soil samples (0–5 cm depth) were collected from the three field sites and measured for gravimetric moisture content (Fig. 5). We also measured initial gravimetric moisture content on the incubation samples (Fig. 5, inset), allowing us to directly compare incubation and in situ soil moisture conditions. Assuming that the % saturation: % gravimetric moisture relations for the incubation and the field are similar, near-surface soils at "Poorly Drained" and "Moderately well Drained" were most often within the ideal 50–75% saturation range for the influence of temperature. Soils at "Well Drained" were usually <50% saturation, except when moisture increased at the end of September.

Effects of soil organic matter chemistry on decomposition

Potential decomposition of SOM at 20°C and 50% saturation was significantly correlated with initial soil C:N ratios for "Poorly Drained" (linear regression, $p < 0.01$, $R^2 = 0.93$). In addition, decomposition of

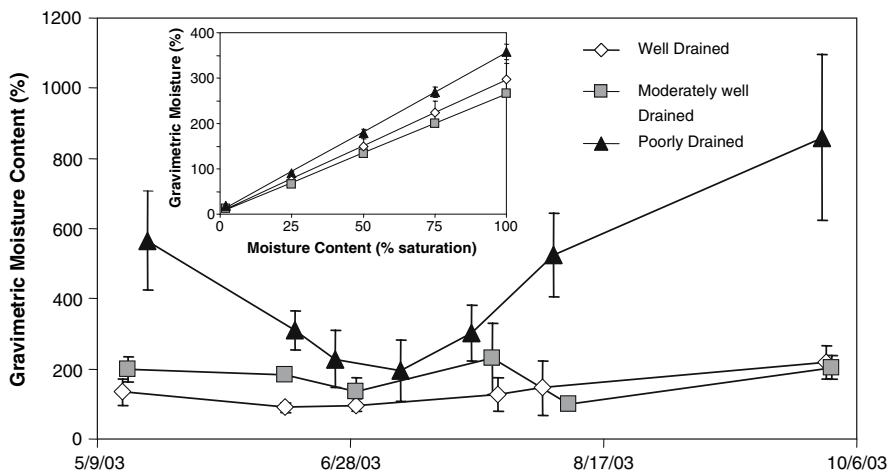

Fig. 5 Mean gravimetric moisture content (±SE) of surface soils (0–5 cm depth) in the field during 2003, and mean gravimetric moisture content (±SE) of soils during incubation (inset). The linear regression equations for the inset graph are: (Well Drained) y = 290.1x+5.0; (Moderately well Drained) y = 260.1x+4.8; and (Poorly Drained) y = 348.8x+7.3 (all equations have $R^2 = 0.99$)

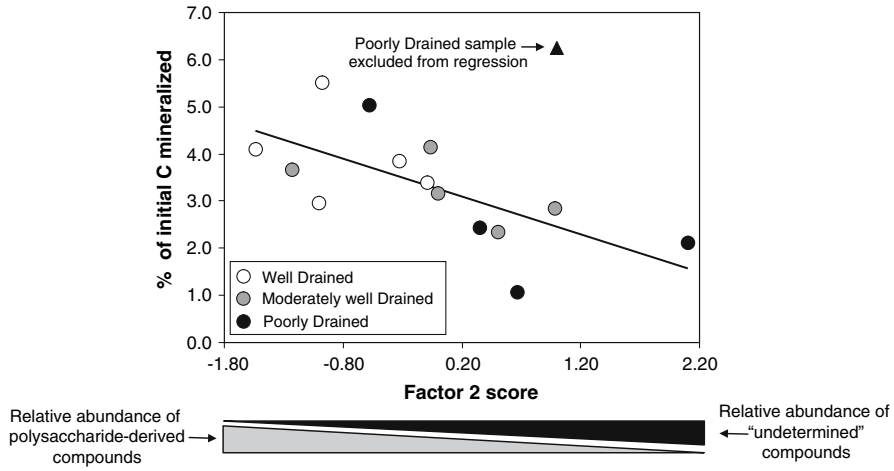

Fig. 6 Total % of initial C mineralized versus PCA factor 2 score for samples incubated at 20°C, 50% saturation. Each point represents one sample. The linear regression equation, which excludes the indicated sample, is: $y = -0.802x + 3.26$, $R^2 = 0.44$. The bar across the bottom indicates relative source compound abundances

"Poorly Drained" SOM under this condition was negatively correlated with initial N content (linear regression, $p = 0.06$, $R^2 = 0.74$), while there was no significant correlation with initial C content. Decomposition of SOM from "Moderately well Drained" and "Well Drained" was not correlated with initial soil C:N or C or N content.

Initial OM chemical characteristics as described by py-GC/MS were a good indicator of potential decomposition across all sites. Potential decomposition (20°C and 50% saturation) was significantly correlated with factor 2 scores from the PCA analysis of py-GC/MS, although one sample from "Poorly Drained" did not follow this relationship (Fig. 6, $F = 9.4$, $p < 0.01$, $R^2 = 0.44$). As factor 2 scores moved from negative (indicating a relative predominance of polysaccharide-derived compounds) to positive (greater relative amount of compounds of "undetermined" source), decomposition decreased. Potential decomposition was significantly correlated with factor 2 scores under incubation conditions 20°C/25% and 20°C/75% saturation when the same sample from "Poorly Drained" was excluded (linear regression, $p < 0.05$). There was no significant relation between potential decomposition and polysaccharide-derived compounds, but there was a negative correlation with the relative abundance of "undetermined" compounds ($F = 8.8$, $p = 0.012$, $R^2 = 0.42$; one "Poorly Drained" sample excluded). However, it was slightly weaker than the correlation with PCA factor 2.

Comparison of pre- and post-incubation (20°C, 50% saturation) py-GC/MS analyses indicates that the mean relative amounts of polysaccharide-derived compounds decreased in "Well Drained" and "Moderately well Drained" samples, while lignin-derived compounds decreased slightly in "Poorly Drained" samples (Table 3). The relative amount of nitrogen compounds decreased in all samples, and there were variable changes in the relative amounts of lipid-derived and "undetermined" compounds.

Decomposition constants and MRT

The single-pool decomposition model (Eq. 1) described 70–98% of the variance in the incubation time series across all sites and conditions (Table 5). The k values were much smaller for soils at 2% saturation than for all other moisture conditions, resulting in MRTs up to 20 times longer compared to more saturated soils. For example, at 2% saturation MRT was 57 ± 9 years (mean ± SE), whereas at 75% saturation MRT was 5 ± 0.6 years across all sites and temperatures. The two-pool decomposition model (Eq. 2) described mineralization better than the single-pool model except for soils at low saturation and for "Moderately well Drained" soils at 10°C, <100% saturation (Table 5). The labile C pool was only a small portion of the total C, accounting for 0.1–2.0% of total C with MRTs ranging from 2 to 27 days. The MRTs for the stable C pools calculated from the two-pool decomposition model were on average two times longer than the MRTs for the single-pool model, and were significantly different from each other (T-test for independent samples, t-value = −3.74, $p = 0.0004$).

Discussion

Soil organic matter originating from black spruce forest sites of widely varying hydrologic and thermal regimes exhibited broad differences in potential decomposition under uniform environmental conditions. Soil organic matter from the "Well Drained" site lost significantly more C to mineralization than SOM from both the "Moderately Well Drained" and the "Poorly Drained" sites, when results were averaged across incubation conditions. Temperature and moisture exerted strong influences on decomposition, and their effects were consistent across all sites despite the site-dependent differences in potential C loss and SOM chemistry. While temperature and moisture controlled decomposition independently of one another, their combined effects acted to mutually constrain potential influences on decomposition. These differences, along with SOM chemistry analyses, suggest that variations in SOM chemical characteristics among the sites lead to inherently different potential decomposition rates in the laboratory.

Temperature and moisture control of soil organic matter decomposition

Very low soil moisture content acted to inhibit decomposition, and to limit the opportunity of temperature to affect decomposition. Dry conditions reduced SOM decomposition to a much greater degree than saturated conditions did in the laboratory incubations, and decomposition showed strong temperature responses only within a soil moisture range of 50–75% saturation. These findings, combined with seasonal changes in field soil moisture content at the three sites, suggest that temperature increases may have more effect on decomposition of near-surface SOM at "Poorly Drained" and "Moderately well Drained" sites than at the "Well Drained" site (Fig. 5). This implies that dry moisture conditions may at times inhibit decomposition of near-surface SOM in sites that undergo strong seasonal changes in soil moisture and prolonged dry periods, and that low moisture may limit the effect of temperature on SOM decomposition. At the same time super-saturated conditions likely inhibit near-surface SOM decomposition in early spring and late fall, particularly at the "Poorly Drained" site, especially if soils become anoxic (Moore and Dalva 1997; Scanlon and Moore 2000).

The relative importance of temperature and moisture controls on decomposition is central to understanding organic matter decomposition in the boreal forest system, and for predicting the effects of climate change on SOM decomposition. Combined effects of temperature and moisture controls on decomposition are significant in temperate soils (Leirós et al. 1999) but there are relatively few studies that include combined analysis of temperature and moisture controls on decomposition in boreal ecosystems. These relations are important to ecosystem models that typically calculate decomposition as a product of soil temperature and moisture conditions (Parton et al. 1987; Frolking et al. 1996, 2001). Our results illustrate that for a range of boreal black spruce systems, temperature and moisture work together in controlling SOM decomposition when soil moisture is in an optimum range, but that temperature has very little or no effect when soil moisture levels are outside of that range. Predictions of the effects of climate change on C cycling at northern latitudes often suggest that warmer, drier conditions will stimulate soil decomposition (Anderson 1991; Oechel et al. 1993; Moore et al. 1998). Warmer temperatures will certainly result in increased decomposition, but if soil moisture contents are too low, conditions that may occur with some frequency in continental black spruce systems, then the effect of temperature will be limited.

Soil organic matter chemistry and decomposition

The best measured predictor of potential SOM decomposition across all sites, with regards to OM structure, was PCA factor 2. This factor was negatively associated with polysaccharide-derived compounds and positively associated with "undetermined" compounds. This indicates that both compound classes play important and contrasting roles in decomposition. Polysaccharides are an important source of energy and C for microbes, and in general they are rapidly degraded in soils (Stevenson and Cole 1999). The cause of the negative correlation between decomposition and the "undetermined" compounds is difficult to determine, as this

category was dominated by unidentifiable compounds and compounds that couldn't be attributed to unique sources. In the case of the unidentifiable compounds, it is possible that complex structures and high molecular weight could reduce decomposition rates or potentially even have an inhibitory effect on decomposition.

The broad differences in SOM chemistry among the sites may result from differences in decomposition stage, decomposition pathways, differences in plant litter chemistry, or a combination of all these factors. However, the patterns of relative abundance of compound classes in this study suggest that OM structural information could be useful in predicting potential decomposition in boreal soils. For example, primary polysaccharides, which include furfural and levoglucosenone as pyrolysates, are preferentially utilized during microbial decomposition in peat soils (Bracewell et al. 1980, 1989). These compounds were 1.5–2 times greater in relative abundance in "Well Drained" and "Moderately well Drained" SOM samples compared to "Poorly Drained" SOM samples, and the drier soils appear to be more decomposable than soil from the "Poorly Drained" site. The cause of these differences in initial structure requires additional study but could be related to differences in litter chemistry and/or differences in decomposition stage across the three sites.

One of the key vegetation differences between sites is the presence of different moss species across the sites. *Sphagnum* mosses, which are present only at "Poorly Drained", are composed of non-lignin compounds that are slow to decompose, such as phenolic compounds, waxes, and polymerized lipids, and they have very little N content (Hobbie 1996; Aerts et al. 1999). Turetsky (2004) attributed differences in organic fractions of surface peat from Canadian bogs (dominated by *Sphagnum fuscum*) and permafrost mounds (dominated by *Pleurozium schreberi* and *Hylocomium splendens*) to differences in botanical composition. The lower average potential decomposition rates of "Poorly Drained" SOM may be due in part to the relatively slow decomposition rates of *Sphagnum* spp. litter (Johnson and Damman 1993; Belyea 1996; Camill et al. 2001). Several mechanisms for the slow rates of *Sphagnum* litter decomposition have been proposed (Turetsky 2003), including poor substrate quality (Aerts et al. 1999), exudation of antibacterial compounds (Verhoeven and Toth 1995; Basile et al. 1999), and the promotion of wet, cold conditions unfavorable for decomposition (Van Cleve et al. 1983).

"Poorly Drained" SOM exhibited the lowest potential decomposition as a group, but there was significant variability among the individual samples. Two of the samples lost significantly more C to mineralization than the other "Poorly Drained" samples, including one of which surpassed all "Well Drained" and "Moderately well Drained" samples in relative C loss (the same sample that did not follow the trend described by py-GC/MS analyses). The large within-site difference in decomposition was strongly related to SOM C:N ratios, where decomposition increased with increasing C:N. This relation could be a result of N effects on early stages of decomposition (Keyser et al. 1978; Erikkson et al. 1990; Berg and Matzner 1997; Berg 2000), or it may be indicative of large differences in prior decomposition in the field (Stevenson and Cole 1999). While determining the source of variation in molecular C structure and its effects on decomposition remains challenging, our results demonstrate that molecular studies may provide new insights into the decomposition processes in boreal forests.

Conclusions

Soil organic matter from boreal black spruce ecosystems representing a wide range of hydrologic and thermal conditions contain a substantial C pool that degrades rapidly under ideal conditions. The rates of potential decomposition were well within the range of rates measured for soils from various temperate ecosystems (Kätterer et al. 1998) and other boreal soils (Neff and Hooper, 2002; Dioumaeva et al. 2003). Temperature and moisture are important independent and additive controls of decomposition, and the combined effects of these variables need to be considered to understand and predict the response of decomposition in boreal ecosystems to climate change. In addition, OM chemical characteristics were indicative of potential decomposition rates in the laboratory under ideal temperature and moisture conditions. Results from this study provide useful information for modeling decomposition of SOM in boreal ecosystems, and potentially for other ecosystems as well. In particular, the decomposition

constants we measured for black spruce SOM, and the response of decomposition to temperature and moisture provide bounds that can applied to future models of these types of systems. In addition, our quantification of the combined effects of temperature and moisture on SOM decomposition may well apply to ecosystems outside of the boreal biome.

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Appendix 1 Compounds identified using pyrolysis-GC/MS

Compound	Source[a]	Type[b]	Site[c]
2-Propanone, 1-(4-hydroxy-3-methoxyphenyl)-	Lg		all
3,4-Dimethoxytoluene	Lg		all
Acetosyringone	Lg		WD, PD
Acetovanillone	Lg		all
Benzene, 1-methoxy-4-methyl-	Lg		MD
Ethanone, 1-(3,4-dimethoxyphenyl)-	Lg		WD, PD
Phenol, 2,6-dimethoxy- (syringol)	Lg		all
Phenol, 2,6-dimethoxy-4-(2-propenyl)-	Lg		all
Phenol, 2-methoxy- (guaiacol)	Lg		all
Phenol, 2-methoxy-4-(1-propenyl)- (isoeugenol)	Lg		all
Phenol, 2-methoxy-4-(2-propenyl)-	Lg		MD, PD
Phenol, 2-methoxy-4-methyl- (methylguaiacol)	Lg		all
Phenol, 2-methoxy-4-propyl-	Lg		all
Phenol, 2-Methoxy-4-vinyl- (vinylguaiacol)	Lg		all
Phenol, 4-ethyl-2,6-dimethoxy- (ethylsyringol)	Lg		WD
Phenol, 4-ethyl-2-methoxy- (ethylguaiacol)	Lg		all
Vanillic acid	Lg		all
Vanillic Acid, methyl ester	Lg		WD, PD
Vanillin	Lg		all
2H-Pyran-2-one	Ps		all
2-Cyclopenten-1-one, 2,3-dimethyl-	Ps		all
2-Cyclopenten-1-one, 2-hydroxy-3-methyl-	Ps		all
2-Cyclopenten-1-one, 2-methyl-	Ps		all
2(3H)-Furanone, 5-methyl-	Ps		all
2(5H)-Furanone	Ps		all
2(5H)-Furanone, 5-methyl-	Ps		all
2,5-Furandione, 3-methyl-	Ps		all
4H-Pyran-4-one, 3-hydroxy-2-methyl-	Ps		all
Furan, 2,3,5-trimethyl-	Ps		all
Furan, 2,5-dimethyl-	Ps		all
Furan, 2-ethyl-	Ps		all
Furan, 2-ethyl-5-methyl-	Ps		all
Furan, 3-methyl-	Ps		all

Appendix 1 continued

Compound	Source[a]	Type[b]	Site[c]
Furfural	Ps		all
Furfural, 5-methyl-	Ps		all
Methyl 2-furoate	Ps		WD
Vinylfuran	Ps		all
2-Acetylfuran	Ps		all
2-Furanmethanol	Ps		all
3-Furaldehyde	Ps		all
Acetic acid, methylester	Ps		all
1,2-Cyclopentanedione	Ps		all
2-Cyclopenten-1-one, 3-methyl-	Ps		WD, MD
Cyclopent-2-ene-1-one, 2,3,4-trimethyl-	Ps		all
Cyclopentanone	Ps		MD
Cyclopropanecarboxaldehyde, methylene-	Ps		all
Levoglucosan	Ps		WD
Levoglucosenone	Ps		all
Methylbutanal	Ps		all
Unknown polysaccharide	Ps		all
1H-Pyrrole, 1-methyl-	N		all
1H-Pyrrole, 2-methyl-	N		all
1H-Pyrrole, 3-methyl-	N		MD
1H-Pyrrole-2-carboxaldehyde	N		all
1H-Pyrrole-2-carboxaldehyde, 1-methyl-	N		all
2-(N-Methyl-N-ethylamino)phenol	N		PD
2-Pyridinealdehyde	N		WD, MD
2-Propyn-1-amine	N		WD
2,5-dimethylpyrrole	N		all
3-Methylindole	N		all
3-Phenylpyridine	N		WD, PD
3-Pyridinol	N		WD, MD
Acetamide, N-hydroxy	N		all
Benzenepropanenitrile	N		all
Benzyl nitrile	N		MD, PD
Dimethylpyrrole (2,5 or 2,4)	N		all
Ethanone, 1-(1-methyl-1H-pyrrol-2-yl)-	N		PD
Piperidine-2,5-dione	N		all
Pyrazolo[5,1-c][1,2,4]benzotriazin-8-ol	N		all
Pyridine	N		all
Pyridine 3-methyl	N		all
Pyridine, 3,5-dimethyl-	N		all
Pyridine, 4-methoxy-	N		PD
Pyridine, methyl- (3/2/4)	N		WD, PD
Pyrrole	N		all
n-Dodecane	Lp		all
n-Eicosane	Lp		all

Appendix 1 continued

Compound	Source[a]	Type[b]	Site[c]
n-Heptadecane	Lp		all
n-Heptane	Lp		PD
n-Nonane	Lp		all
n-Octadecane	Lp		PD
n-Octane	Lp		all
n-Pentadecane	Lp		all
n-Tetradecane	Lp		MD, PD
Tridecane	Lp		all
1,3-Octadiene	Lp		MD
1-Heptene	Lp		MD, PD
1-Hexene, 3-methyl-	Lp		all
1-Pentene, 2-methyl-	Lp		all
Dodecene	Lp		all
Heptadecadiene	Lp		MD
Heptadecene	Lp		WD
1-Hexadecene	Ud	Alkene	MD
7-Tetradecene	Ud	Alkene	all
2-Butanone	Ud	Aliphatic	all
3-Penten-2-one, (E)-	Ud	Aliphatic	all
1H-Inden-1-one, 2,3-dihydro-	Ud	Aromatic	all
2H-1-Benzopyran-2-one	Ud	Aromatic	MD
2-Methoxyresorcinol	Ud	Aromatic	WD, PD
Acetophenone	Ud	Aromatic	MD
Benzene, 1,2,3-trimethyl-	Ud	Aromatic	all
Benzofuran	Ud	Aromatic	all
Benzofuran, 2,3-dihydro-	Ud	Aromatic	all
Benzofuran, 2-methyl-	Ud	Aromatic	all
Biphenyl	Ud	Aromatic	all
Benzaldehyde	Ud	Aromatic	WD, MD
Benzene	Ud	Aromatic	all
Benzene, (1,3-dimethylbutyl)-	Ud	Aromatic	MD
Benzene, (1-methylethyl)-	Ud	Aromatic	PD
Benzene, 1,2-diethyl-	Ud	Aromatic	all
Benzene, 1-ethenyl-3-methyl-	Ud	Aromatic	all
Benzene, 4-ethenyl-1,2-dimethoxy-	Ud	Aromatic	all
Benzene, butyl-	Ud	Aromatic	PD
Benzene, heptyl-	Ud	Aromatic	MD
Benzene, hexyl-	Ud	Aromatic	all
Benzene, propyl-	Ud	Aromatic	all
$C_{11}H_{12}$	Ud	Aromatic	MD
Dimethylbenzofuran	Ud	Aromatic	all
Ethylbenzene	Ud	Aromatic	MD
Fluorene	Ud	Aromatic	PD
Homocatechol	Ud	Aromatic	WD, MD
Indane	Ud	Aromatic	all

Appendix 1 continued

Compound	Source[a]	Type[b]	Site[c]
m-xylene	Ud	Aromatic	all
Resorcinol (dihydroxybenzene)	Ud	Aromatic	all
Styrene	Ud	Aromatic	all
Toluene	Ud	Aromatic	all
Trimethylphenol	Ud	Aromatic	all
D-Limonene	Ud	Aliphatic	all
Pyruvaldehyde	Ud	Aliphatic	all
Unknown aliphatic	Ud	Aliphatic	all
Phenol	Ud	Phenol	all
Phenol, 3,4-dimethyl-	Ud	Phenol	all
Phenol, 3-methyl-	Ud	Phenol	all
Phenol, 4-methyl-	Ud	Phenol	all
C_9H_8	Ud	Ud	MD, PD
Oxirane, ethenyl-	Ud	Ud	all
38 Unidentifiable compounds	Ud	Ud	all

[a] Lg, lignin; Ps, polysaccharide; N, nitrogen compound; Lp, lipid; Ud, undetermined

[b] Type listed for compounds of undetermined source only; Ud, undetermined

[c] WD = Well Drained, MD = Moderately well Drained, PD = Poorly Drained, all = all sites

A site is listed if compound was present in at least one sample from that site

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