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Production of Dissolved Organic Carbon in Canadian Forest Soils

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Abstract

To identify the controls on dissolved organic carbon (DOC) production, we incubated soils from 18 sites, a mixture of 52 forest floor and peats and 41 upper mineral soil samples, at three temperatures (3, 10, and 22°C) for over a year and measured DOC concentration in the leachate and carbon dioxide (CO_2) production from the samples. Concentrations of DOC in the leachate were in the range encountered in field soils (<2 to >50 mg l^{-1}). There was a decline in DOC production during the incubation, with initial rates averaging 0.03–0.06 mg DOC g^{-1} soil C day^{-1}, falling to averages of 0.01 mg g^{-1} soil C day^{-1}; the rate of decline was not strongly related to temperature. Cumulative DOC production rates over the 395 days ranged from less than 0.01 to 0.12 mg g^{-1} soil C day^{-1} (0.5–47.6 mg g^{-1} soil C), with an average of 0.021 mg g^{-1} soil C day^{-1} (8.2 mg g^{-1} soil C). DOC production rate was weakly related to temperature, equivalent to Q_{10} values of 0.9 to 1.2 for mineral samples and 1.2 to 1.9 for organic samples. Rates of DOC production in the organic samples were correlated with cellulose (positively) and lignin (negatively) proportion in the organic matter, whereas in the mineral samples C and nitrogen (N) provided positive correlations. The partitioning of C released into CO_2–C and DOC showed a quotient (CO_2–C:DOC) that varied widely among the samples, from 1 to 146. The regression coefficient of CO_2–C:DOC production ($\log_{10}$ transformed) ranged from 0.3 to 0.7, all significantly less than 1. At high rates of DOC production, a smaller proportion of CO_2 is produced. The CO_2–C:DOC quotient was dependent on incubation temperature: in the organic soil samples, the CO_2–C:DOC quotient rose from an average of 6 at 3 to 16 at 22°C and in the mineral samples the rise was from 7 to 27. The CO_2–C:DOC quotient was related to soil pH in the organic samples and C and N forms in the mineral samples.

Key words: dissolved organic carbon; carbon dioxide; decomposition; soil organic matter; lignin; cellulose.

Introduction

Dissolved organic carbon (DOC) is a complex mixture of organic compounds which plays an important role in terrestrial ecosystems, as a substrate for biological activity, as an acidifying and weathering agent, through its effects on the availability and mobility of nutrients and metals and as a source of carbon in aquatic ecosystems (see Thurman 1985). DOC is produced in the vegetation canopy and the litter and soil organic layers and is adsorbed in mineral soils, so that the export of DOC from most soils is small, generally less than 5 g m^{-2} y^{-1}, although there can be considerable internal production, consumption and retention of DOC within forest ecosystems (see Michalzik and others 2001). Along with hydrology, a primary influence on the flux of DOC within soils is the rate at which DOC is produced and several studies have examined the controls on DOC production (see Kalbitz and others 2000).

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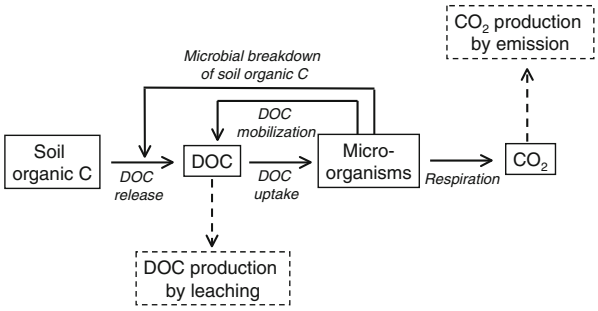


Figure 1. Conceptual model of DOC and CO_2 production in soils (adapted from Bengtson and Bengtsson 2007). Dashed line boxes indicate the DOC and CO_2 production estimated in this study, by water leaching and emission to the atmosphere, respectively.

Neff and Asner (2001) developed a model of DOC in terrestrial ecosystems, DOC being generated by the decomposition and leaching of litter and soil organic matter, with both the biotic and abiotic components. Bengtson and Bengtsson (2007) have recently proposed a model linking the production of DOC and carbon dioxide (CO_2) from soil organic matter breakdown (Figure 1). They have shown in a beech-oak forest soil that CO_2 was derived from DOC, that CO_2 production rate was dependent on DOC production rate and that the DOC pool turned over several times per day. Although DOC can be produced from simple leaching of organic materials, microbial activity is important, both in the uptake from and release to the soil solution of DOC and in the production of enzymes leading to organic matter breakdown. Kemmitt and others (2008) have suggested that the rate of organic matter mineralization is independent of microbial biomass. The soil C and N model proposed by Schimel and Weintraub (2003) regards DOC partly as a microbial ''waste product,'' dependent on the C:N quotient of the substrate.

Laboratory incubations of litter and soils have revealed the influence of the following on DOC production: temperature (for example, Andersson and others 2000; Gödde and others 1996; Moore and Dalva 2001); duration of the incubation, which depletes the DOC pool (for example, Christ and David 1996; Moore and Dalva 2001); soil pH and exchangeable cations (for example, Andersson and others 2000); substrate characteristics such as botanical origin, degree of decomposition, and C:N ratio (for example, Cleveland and others 2004; Don and Kalbitz 2005; Gödde and others 1996; Judd and Kling 2002; Kalbitz and others 2006; Moore and Dalva 2001; Neff and Hooper 2002; O'Connell and others 2000; Park and others 2002); frequency and rate of leaching (for example, Gödde and others 1996; Judd and Kling 2002); oxic or anoxic conditions (O'Connell and others 2000; Moore and Dalva 2001); and microbial community (for example, Møller and others 1999; Park and others 2002). In all of these incubation studies, net DOC production is measured: the difference between the production of DOC and its utilization by the microbial community or sorption on to or from soil particles. DOC degradability can be large (for example, Qualls and Haines 1992; Qualls 2004), so that much of the DOC produced can be rapidly consumed, being incorporated into microbial tissue or released as CO_2, which is part of the partitioning of C released from soils into DOC and CO_2.

Field studies have reported larger DOC concentrations in soil pore-water during the summer, which has been taken to be the evidence of the role of microbial activities and temperature on DOC production rates (for example, Cronan and Aiken 1985; Dai and others 1996; McDowell and Likens 1988).

The objective of this work was to measure the rate of DOC production from soils collected from the organic and upper mineral layers of 16 upland forest sites and two peatland sites, part of the Fluxnet Canada network. These sites represent the major ecological forest groups in Canada and each of the two peatland sites provided samples from a hummock and a hollow. Through laboratory incubations over 1 year, we relate the rates of DOC production to temperature (incubations conducted at 3, 10, and 22°C), to the duration of the incubation, and to the soil characteristics. We also determine rates of CO_2 production and thus the partitioning of C release into DOC and CO_2 and its controls (Figure 1).

Methods

Samples were collected from the forest floor and mineral soil at 18 sites that are part of the Fluxnet Canada Network covering many of the major forest types in Canada. At each site, three plots were located and 15 × 15 cm blocks of the forest floor (F and H horizons) collected, after removal of the litter layer (defined as loose plant material). Samples from the upper mineral soil (mix of A and B horizons) were collected using a borer, to a depth of 20 cm; soils and the sites are characterized in Table 1. At the two peatland sites, hummock and hollow microtopographies were used to sample the upper and lower organic layers, after removal of the litter and live moss layer. Samples were placed in a cooler in the field and transferred to a cold

Table 1. Characteristics of the Soils, by Vegetation, Soil Type (CANSIS), pH (in 0.01 M $CaCl_2$), Organic C and Total N Concentration, and C:N Quotient, Based on the Mean of Between 1 and 3 Replicates per Sample

Site	Dominant vegetation	Soil type	Sample	pH	Org. C (%)	N (%)	C:N quotient
ON-HMW03	Mixed wood harvested 2003	Humo-ferric podzol	Organic	4.63	50.76	1.39	36.7
			Mineral	4.89	1.57	0.05	28.9
ON-OMW	Mature mixed wood	Orthic brunisol, dystric gleysol	Organic	4.36	49.30	1.77	27.8
			Mineral	5.58	0.59	0.02	26.5
QC-HBS00	Black spruce (*Picea mariana*) harvested 2000	Podzol	Organic	4.35	50.98	1.06	46.0
			Mineral	4.73	4.87	0.14	34.3
QC-EOBS	Mature black spruce (*P. mariana*)	Podzol	Organic	4.33	44.98	0.74	61.0
			Mineral	4.78	0.96	0.02	58.8
SK-HJP02	Jack pine (*Pinus banksiana*) harvested 2002	Orthic eutric brunisol	Mineral	5.90	0.32	0.00	97.5
SK-F89	Jack pine (*P. banksiana*) fire 1989	Dystric brunisol	Organic	4.37	14.29	0.52	27.4
			Mineral	4.81	0.32	0.02	16.1
SK-NOBS	Mature black spruce (*P. mariana*)	Gleyed eluviated eutric brunisol	Organic	5.66	40.40	1.83	22.1
SK-NOBS-H			Organic	4.57	41.42	1.72	24.1
SK-NOBS			Mineral	5.86	0.72	0.03	25.5
SK-OJP	Mature jack pine (*P. banksiana*)	Orthic Eutric Brunisol	Organic	4.97	20.71	0.63	32.8
SK-OJP			Mineral	5.86	0.53	0.01	55.8
SK-OA	Mature aspen (*Populus tremuloides*)	Orthic gray luvisol	Organic	6.06	37.54	1.87	20.1
SK-OA			Mineral	6.18	0.98	0.07	13.5
BC-HDF00	Douglas fir (*Pseudotsuga menziesii*) harvested 2000	Humo-ferric Podzol	Organic	5.64	25.66	0.78	32.9
			Mineral	5.71	2.92	0.10	30.0
BC-HDF88	Douglas fir (*P. menziesii*) harvested 1988	Humo-ferric podzol	Organic	4.42	32.19	0.66	49.0
			Mineral	4.73	5.08	0.14	36.3
BC-HDF48	Mature Douglas fir (*P. menziesii*) 1948	Humo-ferric podzol	Organic	5.16	36.94	0.87	42.5
			Mineral	5.44	6.45	0.17	37.7
NB-HBF03	Balsam fir (*Abies balsamea*) cut 2003	Humo-ferric podzol	Organic	4.25	45.11	1.23	36.8
			Mineral	4.51	2.55	0.18	14.4
NB-OBF	Mature balsam fir (*A. balsamea*)	Humo-ferric podzol	Organic	4.13	45.15	1.31	34.5
			Mineral	4.20	3.08	0.13	24.4
SK-F98	Jack pine (*P. banksiana*) fire 1998	Dystric brunisol	Organic	5.17	29.36	1.01	29.1
			Mineral	5.53	0.18	0.01	17.7
SK-F77	Black spruce and Jack pine (*P. banksiana*) fire 1997	Dystric brunisol	Organic	3.31	19.48	0.46	42.8
			Mineral	4.30	0.40	0.02	19.8
AB-WPL	Stunted *Larix laricina*, and *P. mariana*, shrubs and mosses	Fibrisol	Peat—hollow	5.75	47.83	2.37	20.2
			Peat—hummock	5.21	46.71	1.26	37.0
ON-EPL	Shrubs and mosses	Fibrisol	Peat—hollow	4.55	46.45	0.91	51.1
			Peat—hummock	4.25	46.64	0.77	60.5

room (3°C). The samples were sieved through 6- and 4-mm screens for the forest floor and mineral samples, respectively, to allow homogenization whilst retaining some of the soil structure.

The incubation system was similar to that employed by Nadelhoffer and others (1991). The soil material was weighed to obtain samples of about 25 g of fresh forest floor and 100 g of fresh mineral soil and inserted into 150 ml plastic containers above a layer of pre-washed (0.01 M HCl and deionized water) glass wool. The bottom lid consisted of a plastic screen. The soil material was then packed slightly to obtain a total soil volume of 70 and 100 cm^3, for the organic and mineral layers, respectively. The plastic containers sat on the top section of a filtration system. A total of 279 individual soil samples were incubated, representing replicates of each layer at each site and at three temperatures (3, 10, and 22°C). In some analyses, we use the overall mean for all samples incubated, in others the mean of the samples collected at each site, and in others we use the results for the individual soil samples.

These soil microcosms were first leached with 100 ml of 0.005 M K_2SO4 and the excess leachate removed by applying a suction of 0.6 centibars to ensure that all the soils were near field capacity when the incubation was started. The microcosms were leached again with the same solution after 24, 49, 104, 151, 206, 248, 296, and 398 days. The samples remained near field capacity throughout the incubation, based on occasional weighing and rewetting with deionized water. The leachates were filtered through 0.45 μm paper and concentration of DOC determined with a Shimadzu 5050 TOC analyzer.

Measurements of CO_2 production were made after 5, 12, 18, 32, 48, 67, 97, 138, 180, 223, 264, 313, and 411 days by sealing the microcosms in a 500-ml glass jar and measuring changes in CO_2 concentration within the headspace over a period of 24 h, determined with an infrared gas analyzer. More details on CO_2 measurements are given in Paré and others (2006).

Production rates of DOC and CO_2 were calculated on a daily basis and were normalized against C contained in the sample, based on C concentration and initial dry weight at the beginning of incubation.

Soil pH was analyzed in distilled water and $CaCl_2$ (Carter 1993). Total C and N were determined by wet digestion and analyzed with a LECO CNS-2000 analyzer (LECO Corporation 2003). The forest floor samples were analyzed for proximate fractions using the methodology outlined by Ryan and others (1990) and for acid hydrolyzable fractions by Paul and others (2001).

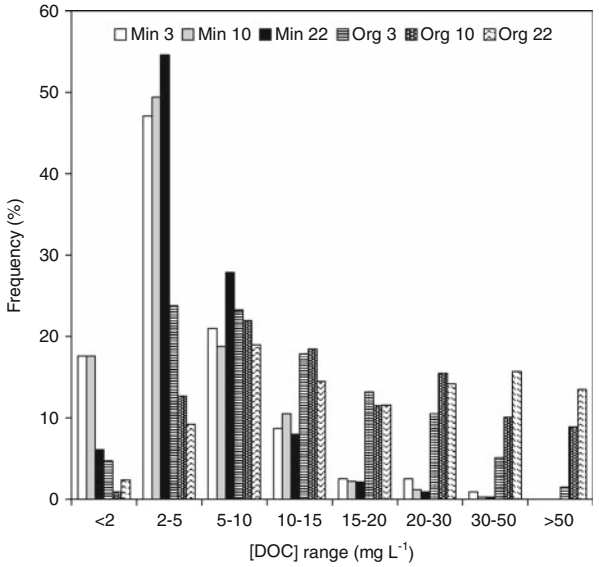


Figure 2. Frequency of DOC concentrations determined in leachates, categorized by temperature and soil type. In this and following figures, Min = mineral soil samples, Org = organic soil samples; 3, 10, and 22 = incubated at 3, 10, and 22°C.

Results

The concentration of DOC in the leachates ranged from less than 2 to more than 50 mg l^{-1}, with concentrations larger in organic than mineral soils and generally larger in samples incubated at the warmer temperatures (Figure 2). These concentrations are similar to those found in soil porewaters under field conditions (see Michalzik and others 2001).

Rates of DOC Production and Controls

There was a general decline, following a logarithmic pattern, in the rate of DOC production through the 395-day incubation period, when organic and mineral samples were grouped together by temperature (Figure 3). Average initial rates, from the leachate collected 24 days after the incubation started, were between 0.03 and 0.06 mg g^{-1} soil C day^{-1} and fell to 0.01 mg g^{-1} soil C day^{-1} by the final leachate collected after 395 days of incubation. There was an increase in the DOC production rates, particularly in the organic samples, in the leachates collected after days 248 and 296, but there is no apparent reason for this. Cumulative DOC production over 395 days ranged from 0.5 to 47.6 mg g^{-1} soil C, with an average of 8.2 mg

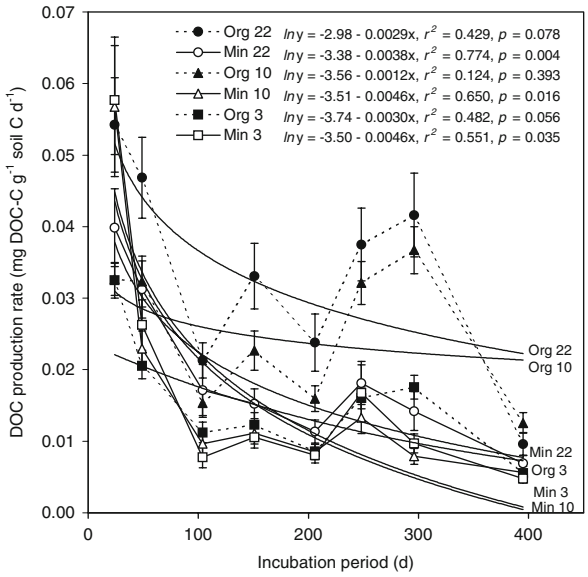


Figure 3. Change in rate of DOC production during the incubation period, with the day indicating the time of leaching. *Bars* indicate standard error of samples incubated at 3, 10, or 22°C for organic and mineral samples (n = 40–51 for each temperature). *Solid curved lines* are logarithmic regressions, indicated in the figure.

DOC g^{-1} soil C (Table 2). There was a strong correlation between the initial (24-day) and cumulative (395-day) rates of DOC production (overall, log_{10}-transformed, $r^2 = 0.61$, $n = 279$, $p < 0.001$). However, because of the variations within these, we use both the initial and cumulative production rates in some of the following discussions.

When organized by temperature and organic/mineral type, there was little increase in average cumulative DOC production for the mineral samples (6.1, 5.7, and 7.3 mg g^{-1} soil C at 3, 10, and 22°C, respectively), equivalent to Q_{10} values of 0.9 (10 vs 3°C) and 1.2 (22 vs 10°C) (Figure 4). Average DOC production in the organic samples increased from 5.9 to 10.2 and 12.8 mg g^{-1} soil C at 3, 10, and 22°C, equivalent to Q_{10} values of 1.9 and 1.2. Cumulative DOC production for individual soils by temperature showed a wide range and a variety of quotients at the incubation temperatures (Table 2). A similar pattern of temperature dependence was found with the initial, 24-day DOC production rates (Figure 4).

When separated into the three incubation temperatures, DOC production rates over 24 and 395 days showed weak relationships with soil properties. For the organic samples, DOC production was most strongly correlated positively and negatively with the proportion of cellulose and lignin in the organic matter, respectively, as illustrated for lignin in Figure 5. When combined into stepwise regressions of DOC production rate over 24-day or cumulative periods and the three incubation temperatures, the coefficient of determination was generally low but significant (r^2 = 0.15–0.44, $p < 0.01$) with lignin or cellulose or cellulose/lignin + cellulose ratio being dominant (Table 3). In the mineral soil samples, DOC production rates were negatively correlated with C, N, hydrolyzable C, and hydrolyzable N concentrations and stepwise regressions resulted in r^2 = 0.26–0.48 ($p < 0.001$).

Partitioning of Released C into CO_2 and DOC

Overall rates of CO_2–C production declined with time with average initial rates between 0.1 and 0.8 mg g^{-1} soil C day^{-1} falling to between less than 0.1 and 0.3 mg g^{-1} soil C day^{-1}. Rates of decline were fastest in samples incubated at 22°C, compared a slower decline at 10 and 3°C (see Paré, pers. comm.). When the average 24- and 395-day CO_2 production rates are compared by temperature, Q_{10} values fell into the range of 1.8 to 3.6, higher than those for DOC production, under the same conditions.

The relationship between DOC and CO_2 production was strong, but there was some variability: overall r^2 values were 0.12 for 24-day and 0.30 for 395-day incubations, but both cases were very significant (log_{10} transformed, $p < 0.001$, $n = 279$). The partitioning of C released into DOC and CO_2, as measured by the CO_2–C:DOC production quotient, showed no significant variation with time during the incubation at 3 and 10°C, but the pattern was more variable for samples incubated at 22°C with a general increase in the later stages of the incubation (Figure 6). The 24- and 395-day CO_2–C:DOC production quotients showed a strong overall dependence on temperature by soil type (Figure 7). In the organic samples, the average quotient rose from 6 at 3°C to 16 at 22°C. The rise was more pronounced in the mineral samples, from an average of 7 at 3°C to 27 at 22°C. Q_{10} values for the CO_2–C:DOC production quotient ranged from 1.6 to 4.0.

For individual soil samples, the 24- and 395-day CO_2–C:DOC production quotients varied greatly, from 1 to 100 (Figure 8). When regression was applied to soils categorized by type (organic or mineral) and temperature with log_{10} transformed production rates, lines with different intercepts were created (22 > 10 > 3°C). The slopes of these regressions were similar, ranging from 0.3 to 0.7 (CO_2–C per DOC) and all significantly less than 1.

Table 2. Cumulative DOC Production over 395 Days (mg g org C soil^{-1}) by Soil and Incubation Temperature (°C) and Quotient of Production Rate among Temperatures (Q_{10})

Soil	Sample	Temperature			Temperature quotients (Q_{10})		
		3	10	22	10 vs 3	22 vs 3	22 vs 10
ON-HMW03	Organic	5.57 (0.95)	10.69 (3.86)	13.73 (9.35)	1.9	2.5	1.3
	Mineral	3.68 (0.52)	2.63 (1.01)	3.73 (1.23)	0.7	1.0	1.4
ON-OMW	Organic	5.34 (2.26)	10.82 (0.73)	10.24 (4.35)	2.0	1.9	0.9
	Mineral	8.69 (3.47)	5.04 (3.92)	8.93 (3.73)	0.6	1.0	1.8
QC-HBS00	Organic	2.65 (0.31)	5.57 (0.73)	6.05 (1.47)	2.1	2.3	1.1
	Mineral	2.48 (1.66)	3.07 (2.16)	3.42 (2.61)	1.2	1.4	1.1
QC-EOBS	Organic	1.86 (0.63)	3.16 (0.73)	4.19 (0.38)	1.7	2.2	1.3
	Mineral	5.72 (1.11)	5.27 (0.08)	6.44 (0.67)	0.9	1.1	1.2
SK-HJP02	Mineral	10.04 (1.28)	10.35 (1.84)	12.30 (1.40)	1.0	1.2	1.2
SK-F89	Organic	2.63	7.69	17.92	2.9	6.8	2.3
	Mineral	4.82	7.04	10.12	1.5	2.1	1.4
SK-NOBS	Organic	2.51 (0.73)	4.45 (0.15)	2.66 (0.56)	1.8	1.1	0.6
SK-NOBS-H	Organic	11.18 (0.34)	17.65 (4.87)	23.91 (9.35)	1.6	2.1	1.4
SK-NOBS	Mineral	4.47 (0.49)	6.44 (0.99)	10.41 (1.26)	1.4	2.3	1.6
SK-OJP	Organic	10.93 (2.54)	19.83 (6.00)	29.83 (17.17)	1.8	2.7	1.5
SK-OJP	Mineral	7.92 (3.00)	9.81 (3.62)	14.03 (4.56)	1.2	1.8	1.4
SK-OA	Organic	6.59 (1.80)	7.78 (1.57)	6.96 (2.06)	1.2	1.1	0.9
SK-OA	Mineral	4.15 (0.49)	4.26 (0.46)	4.75 (0.72)	1.0	1.1	1.1
BC-HDF00	Organic	4.82 (0.74)	9.77 (2.14)	8.01 (1.81)	2.0	1.7	0.8
	Mineral	1.87 (0.55)	1.51 (0.43)	1.30 (0.30)	0.8	0.7	0.9
BC-HDF88	Organic	3.23	3.15	4.85	1.0	1.5	1.5
	Mineral	0.87	0.75	0.54	0.9	0.6	0.7
BC-HDF48	Organic	14.76 (1.54)	28.77 (5.44)	18.85 (10.17)	1.9	1.3	0.7
	Mineral	0.96 (0.34)	1.16 (0.04)	1.15 (0.20)	1.2	1.2	1.0
NB-HBF03	Organic	3.52 (0.44)	6.55 (0.25)	6.36 (1.82)	1.9	1.8	1.0
	Mineral	3.54 (0.07)	3.19 (0.15)	2.35 (0.46)	0.9	0.7	0.7
NB-OBF	Organic	6.04 (2.57)	12.43 (2.37)	14.19 (8.78)	2.1	2.3	1.1
	Mineral	8.15 (4.71)	6.36 (2.08)	4.60 (1.86)	0.8	0.6	0.7
SK-F98	Organic	7.20 (2.16)	10.85 (2.81)	8.47 (2.87)	1.5	1.2	0.8
	Mineral	17.62 (13.28)	15.55 (11.14)	20.89 (11.92)	0.9	1.2	1.3
SK-F77	Organic	8.05	16.27	19.96	2.0	2.5	1.2
	Mineral	7.57	6.91	8.36	0.9	1.1	1.2
AB-WPL	Peat—hollow	2.89 (0.50)	3.01 (0.73)	3.63 (1.31)	1.0	1.3	1.2
	Peat—hummock	5.67 (2.15)	8.72 (4.89)	13.53 (8.96)	1.5	2.4	1.6
ON-EPL	Peat—hollow	5.11 (0.31)	8.44 (0.40)	20.78 (4.15)	1.7	4.1	2.5
	Peat—hummock	5.28 (0.64)	8.92 (0.85)	24.73 (11.97)	1.7	4.7	2.8

Standard deviation of the duplicate or triplicate samples for the organic or mineral soil at each site is indicated in parentheses, except in those cases where only one sample was incubated.

This means that at fast rates of C release, more DOC is produced relative to CO_2 than at slow rates of C release.

In the organic samples, the CO_2–C:DOC production quotient was significantly and positively correlated with soil pH. Stepwise regressions revealed coefficients of determination (R^2) ranging from 0.31 to 0.46 ($p < 0.001$), with a variety of other properties included after pH, depending on the temperature and incubation length (Table 3). In the mineral samples, there were significant positive correlations with hydrolyzable C and N, total C and N concentrations, and pH; stepwise regressions resulted in R^2 values greater than 0.43 (Table 4).

Discussion

As with most laboratory experiments, the applicability of our results is constrained by differences from field conditions. The organic samples, for example, did not receive the input of fresh organic matter from litter or roots, as would occur in the

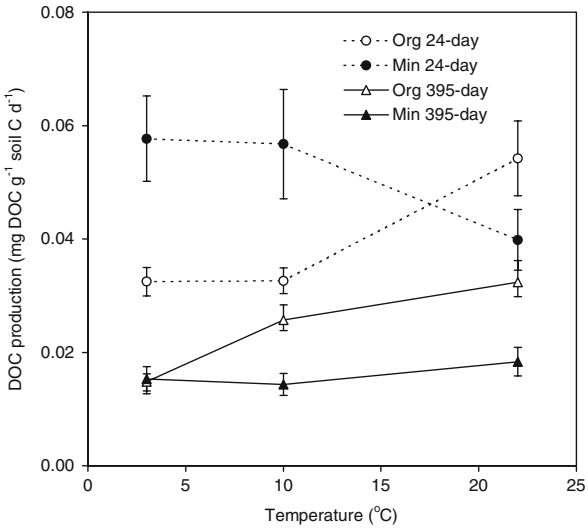


Figure 4. Initial 24-day and cumulative 395-day DOC production, categorized by temperature at 3, 10, and 22°C and soil type. *Bars* indicate standard error (n = 42–51 for each treatment).

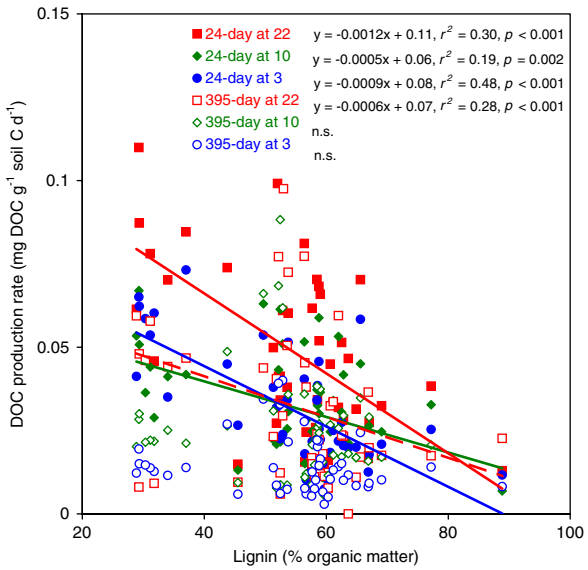


Figure 5. Relationship between cumulative DOC production over the 24- and 395-day incubation periods and the proportion of the organic matter as lignin in the organic samples at the three incubation temperatures (3, 10, and 22°C). *Thin lines* represent the relationship for 395-days and *bold lines* for 24-days. Caption for color online: Relationship between DOC production over the 24- and 395-day incubation periods and the proportion of the organic matter as lignin in the organic samples at the three incubation temperatures (3, 10, and 22°C, *blue, green and red symbols and lines*). *Dashed lines* represent the relationship for 395-days and *bold lines* for 24-days.

field, and both organic and mineral samples were treated with water with negligible DOC concentration, whereas field layers would receive water with higher DOC concentrations. Thus, the samples showed a decrease in DOC production rate with time during the incubations, associated with the depletion of the organic matter contributing to the DOC and CO_2 production pools. In the organic samples, the combined DOC and CO_2 production released a daily average of 0.14–0.78 mg C g^{-1} soil C over 24 days, declining to an average of 0.09–0.30 mg C g^{-1} soil C over 395 days. For the organic samples, assuming an annual soil temperature of about 10°C, these incubations suggest that the forest floor would produce annually an average of between 15 and 25 g DOC m^{-2}, based on a forest floor mass of 2 kg C m^{-2}. This is in the range observed in forest floor leaching in similar forests (see Michalzik and others 2001; Neff and Asner 2001) and combined with the DOC concentrations being similar to field observations (Figure 2) suggest that the laboratory incubations may be similar to field conditions. However, fluxes of DOC in soils are dependent, not only on rates of DOC production, but also on rates of biodegradation and leaching by water, so that our results in absolute terms must be regarded with caution, although differences among samples should be consistent because of the standardized laboratory treatments. In the organic soil samples, the average percentage of the soil organic C lost, by combined DOC and CO_2 production, over 1 year at 10°C was 7% (SD 4) similar to the 11% average reported for Alaskan soils by Neff and Hooper (2002).

Most samples showed a decline in DOC production with incubation duration, so that rates after 1 year were about one-fifth that of the first month. This decline is similar to that observed in fresh tissues, such as leaves and leaf litter, over a shorter period of incubation (for example, Cleveland and others 2004; Moore and Dalva 2001), but is greater than observed during the 1-year incubation of Alaskan soils at 10 and 30°C by Neff and Hooper (2002). The latter observed a temporal increase in DOC production (based on increases in DOC concentration in the leachate) in some cases and there was an increase in overall DOC production of the organic samples incubated at 10 and 22°C in our study, although there is no clear explanation for this.

It is important to note that even at low temperatures, such as 3°C, substantial amounts of DOC and CO_2 can be released by these forest soils: over 1 year, an average of 3.1% (SD 2.2) of the soil C was released from the organic samples. There was a weaker dependence of DOC production on temperature than for CO_2 production, which relates to the origin of the DOC. DOC may be released into

Table 3. Multiple Regression Between DOC Production (in μg DOC g^{-1} soil C day^{-1}) and CO_2–C:DOC Quotient over 24 and 395 Days and at 3, 10, and 22°C and Properties of the Organic Soil Samples (n = 50)

Temperature (°C)	24-day	395-day
DOC production		
3	=43.5 + 1.24*POL − 40.9*LIG/LIG&CELL	=47.2 − 0.52*LIG
	R^2 = 0.152, p = 0.027	R^2 = 0.146, p = 0.008
10	=69.7 + 0.92*POL − 83.6*LIG/LIG&CELL	=26.4 − 0.29*LIG
	R^2 = 0.437, p < 0.001	R^2 = 0.161, p = 0.005
22	=76.4 + 1.26*N − 1.96*LIG	=54.2 + 6.42*NON-POL − 0.94*LIG
	R^2 = 0.370, p < 0.001	R^2 = 0.403, p < 0.001
CO_2–C:DOC quotient		
3	=−0.50 − 0.13*C − 3.08*N + 4.95*pH$CaCl_2$	=−41.6 + 0.22*N + 11.2*pHH_2O − 3.7*pH$CaCl_2$
	R^2 = 0.435, p < 0.001	R^2 = 0.390, p < 0.001
10	=−5.4 − 3.5*N + 2.5*pH$CaCl_2$ + 0.1*LIG	=−14.2 + 3.6*pHH_2O − 0.05*C:N
	R^2 = 0.458, p < 0.001	R^2 = 0.400, p < 0.001
22	=34.1 − 0.28*C − 2.50*NON-POL	=−13.6 + 4.55*pHH_2O + 0.18*C:N − 1.72*NON-POL
	R^2 = 0.307, p < 0.001	R^2 = 0.333, p = 0.001

Soil properties included C and N concentration (%), C:N quotient (C:N), hydrolyzable C content (%), hydrolyzable N content (%), soil pH in water (pHH_2O), and 0.01 M $CaCl_2$ (p$HCaCl_2$), hydrolyzable C/total C, hydrolyzable N/total N, non-polar fraction (NON-POL) (%), polar fraction (POL) (%), cellulose (%), lignin (LIG) (%), and cellulose/(lignin + cellulose) (LIG/LIG&CELL).

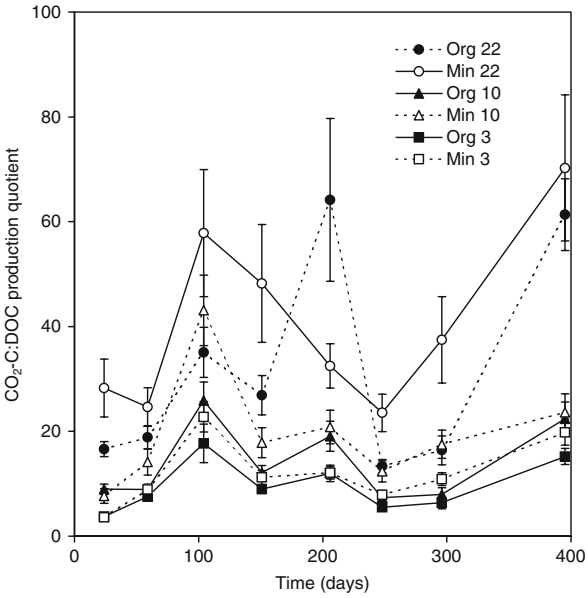


Figure 6. Partitioning of C released into DOC and CO_2, as CO_2–C:DOC quotient, as a function of temperature (3, 10, and 22°C), soil type and length of incubation.

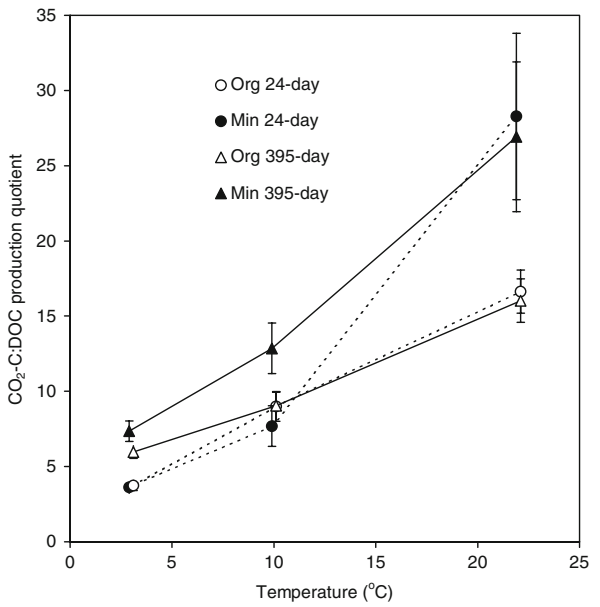
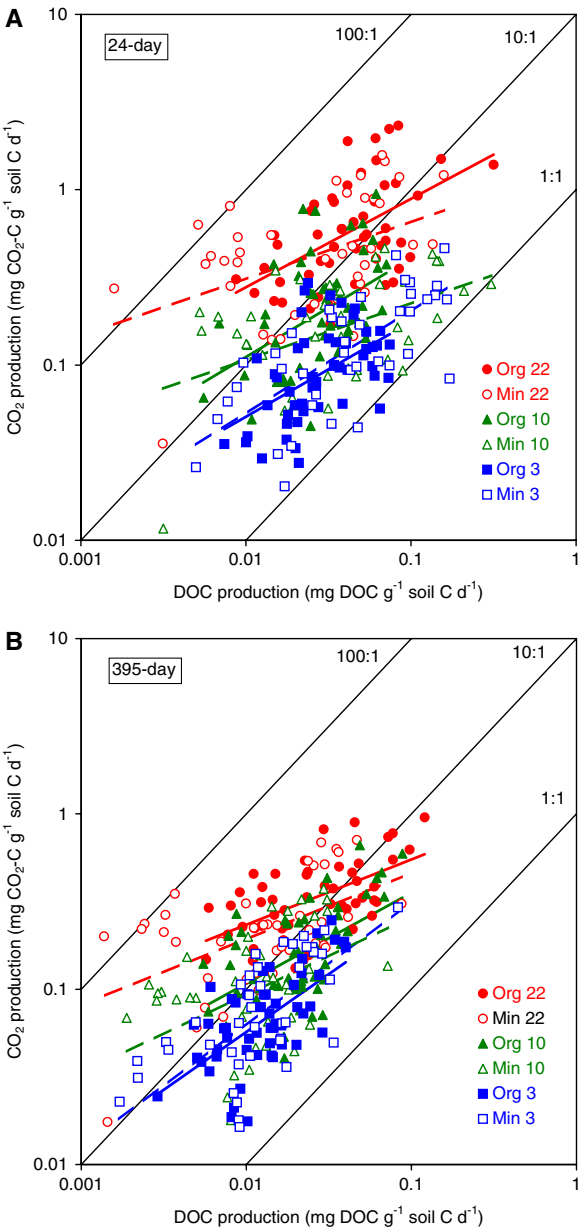


Figure 7. Initial, 24-day and cumulative, 395-day CO_2–C:DOC production quotient, categorized by temperature at 3, 10, and 22°C and soil type. *Bars* indicate standard error (n = 42–51 for each treatment).

the soil solution through direct solution or leaching, through desorption from soil surfaces and through the generation of DOC by microbial processes (Figure 1). This contrasts with CO_2 production, which is primarily microbial in origin and has Q_{10} values commonly in the range of between 2 and 3, as observed in our study, as well as several others, such as Neff and Hooper (2002) who reported increases in CO_2 production rates of Alaskan soil samples of between 4.3 and 5.7 times after 40 days and 1.7 and 3.2 times after 1 year at 30°C compared to 10°C. The smaller temperature dependence of DOC production, between 0.5 and 3.2 times over 10°C, has also been noted by Christ and David (1996), Gödde and others (1996), Moore



◀ **Figure 8.** Initial, 24-day (**A**) and cumulative, 395-day (**B**) CO_2–C and DOC production. *Diagonal lines* represent 100:1, 10:1, and 1:1 ratios of CO_2–C:DOC production. Regressions of log_{10}-transformed data at 3, 10, and 22°C are represented by *lines*, normal for mineral samples and *bold* for organic samples. The *lowest lines* represent samples incubated at 3°C and the *highest lines* at 22°C, with 10°C generally intermediate. Coefficients of determination ranged between 0.21 and 0.54, all significant at $p < 0.005$. Regression coefficients ranging from 0.33 to 0.70 and are all <1.0 at $p < 0.05$ level. Caption for color online: Initial, 24-day (**A**) and cumulative, 395-day (**B**) CO_2–C and DOC production. *Diagonal lines* represent 100:1, 10:1, and 1:1 ratios of CO_2–C:DOC production. Regressions of log_{10}-transformed data at 3, 10, and 22°C (*blue, green and red*, respectively) are represented by *lines*, *dashed* for mineral samples and *solid* for organic samples. Coefficients of determination ranged between 0.21 and 0.54, all significant at $p < 0.005$. Regression coefficients ranging from 0.33 to 0.70 and are all significantly <1.0 at $p < 0.05$% level.

and Dalva (2001), and Neff and Hooper (2002). Davidson and Janssens (2006) reviewed the temperature sensitivity of organic matter decomposition, and noted that there is considerable variability in this sensitivity, related to organic matter and environmental characteristics.

In their study of DOC and CO_2 production from a mineral forest soil in short-term incubations, Bengston and Bengtsson (2007) estimated that DOC release from the soil was 78 mg C kg^{-1} day^{-1}, that CO_2 emission was 149 mg C kg^{-1} day^{-1} and that the microbial community took up and released 261 and 112 mg C kg^{-1} day^{-1}, respectively. Thus, at steady state, the CO_2–C:DOC production quotient was about 2 and they suggest that the overall DOC pool turned over several times per day. Infrequent removal by leaching of the DOC pool would raise this quotient, as the DOC pool would be used to generate CO_2, and in our study, the DOC was leached infrequently. In soils, the temperature sensitivity of DOC release by enzyme reactions may be less than the utilization of DOC by microbes to produce CO_2, resulting in the increase in CO_2–C:DOC production quotient with warmer temperatures (Kemmitt and others 2008).

The differences in mechanisms producing DOC thus create differences in the response to temperature, compared to CO_2, although there is a strong relationship between DOC and CO_2 production rates in our samples, as noted also by Neff and Hooper (2002). The consequence of this differential temperature response is that the partitioning of C released into CO_2 and DOC is also temperature dependent, with high CO_2–C:DOC values at high temperatures. There are differences in the temperature dependence of DOC production by type of soil. DOC production quotients of the incubation temperatures were higher in the organic than mineral soil samples, with *t*-test significant differences ($p < 0.001$) for 10 vs 3°C and 22 vs 3°C, but not 22 vs 10°C ($p < 0.161$) (Table 2). This is again the evidence of the importance of biological production (organic samples) versus desorption (mineral samples) in DOC release.

It is disappointing that DOC production rate, normalized to C, was not strongly and consistently

Table 4. Multiple Regression Between DOC Production (in μg DOC g^{-1} soil C day^{-1}) and CO_2–C:DOC Quotient over 24 and 395 Days and at 3, 10, and 22°C and Properties of the Mineral Soil Samples (n = 41)

Temperature (°C)	24-day	395-day
DOC production		
3	=102 − 468*N − 75*HYDC/TOTC − 92*NHYD/TOTN	=41 − 3*C + 23*pHH_2O − 33*p$HCaCl_2$
	R^2 = 0.481, p < 0.001	R^2 = 0.422, p < 0.001
10	=92–515*N	=24–0.91*N − 23*HYDC/TOTC + 29* HYDN/TOTN
	R^2 = 0.260, p = 0.001	R^2 = 0.357, p = 0.001
22	=105 − 25*C + 21*HYDC − 68* HYDC/TOTC	=29 − 159*N
	R^2 = 0.410, p < 0.001	R^2 = 0.366, p < 0.001
CO_2–C:DOC quotient		
3	=−11 − 1.1*HYDC + 98*HYDC + 2.6* p$HCaCl_2$ + 3.3*HYDN/TOTN	=−24 + 1.3*HYDC + 6.5*p$HCaCl_2$
	R^2 = 0.688, p < 0.001	R^2 = 0710, p < 0.001
10	=−29 + 176*HYDN + 7.5*p$HCaCl_2$	=−37 + 3.8*HYDC + 9.5*p$HCaCl_2$
	R^2 = 0.510, p < 0.001	R^2 = 0.570, p < 0.001
22	=−120 + 640*HYDN + 30*p$HCaCl_2$	=−97 + 611*HYDN + 23*p$HCaCl_2$
	R^2 = 0.431, p < 0.001	R^2 = 0.542, p < 0.001

Soil properties included C and N concentration (%), C:N quotient, hydrolyzable C content (HYDC) (%), hydrolyzable N content (HYDN) (%), soil pH in water (pHH_2O) and 0.01 M $CaCl_2$ (p$HCaCl_2$), hydrolyzable C/total C (HYDC/TOTC), and hydrolyzable N/total N (HYDN/TOTN).

related to soil chemical properties. This is perhaps not surprising, given the diversity of substances comprising DOC and the range of soil samples that we used. Although degree of decomposition has been related to DOC production (for example, Currie and Aber 1997; Don and Kalbitz 2005; Moore and Dalva 2001), our organic samples were all well decomposed. No one chemical analysis provided a strong predictor of DOC production rates, although the positive relationship to cellulose and negative relationship to lignin in the organic samples suggest that these are the major components of the proximate analysis controlling DOC production in organic layers. Kalbitz and others (2006) have recently shown the complex and variable relationship between DOC production and lignin and its degradation in leaf litters. Currie and Aber (1997) partitioned C loss into DOC and CO_2 based on the proximate composition, for example lignocellulose and cellulose fractions, of decomposing litter and soil organic matter. Neutron magnetic resonance analysis of the organic samples also failed to establish a strong relationship with DOC production (S. Quideau, personal communication). In the mineral samples, the amount of soil C and N was negatively related to DOC production rates, without a clear explanation.

Soil C:N has been related to DOC production in some studies (for example, Gödde and others 1996; Kalbitz and Knappe 1997), but not in others (for example, Michel and Matzner 1999) and it has been inferred to be a control on stream and river DOC export (for example, Aitkenhead and McDowell 2000). In the incubation of Alaskan soils, Neff and Hooper (2002) noted that DOC production was initially related (p = 0.05) to soil C:N ratio, but that this relationship disappeared (p = 0.61) when the soils were incubated for a year. There is little evidence in our study to suggest that soil C:N ratio is a primary control on DOC production rate.

Although there was a strong relationship between DOC and CO_2 production in our study, similar to that observed by Moore and Dalva (2001) and Neff and Hooper (2002), there were distinct differences in the partitioning of C release into DOC and CO_2, with a wide range observed among the samples, incubation temperatures and length of incubation. The CO_2–C:DOC quotient increased with higher incubation temperatures and duration of incubation and fell in those samples with fast rates of C release. Moore and Dalva (2001) noted a similar range of CO_2–C:DOC quotients (from 1 to 10) and a decline in the quotient at higher C release rates. During the incubation of Alaskan soils, Neff and Hooper (2002) observed an overall increase in the CO_2–C:DOC quotient from 10 to 30°C (ranging from 12 to 18 and 9 to 30, respectively) and that, at 30°C, this quotient was highest in soil samples with the lowest C release rates. Soil pH and C and N

provided the best predictors of CO_2–C:DOC quotient.

This study has shown that the production of DOC can form a significant proportion of the C released during the decomposition of forest soils and that the rates of DOC production and the partitioning into DOC and CO_2 are controlled by temperature and the composition of the substrate. These results form the basis for the incorporation of DOC production and flux into ecosystem and soil C models, such as proposed by Neff and Asner (2001).

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