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SOME CONTROLS ON THE RELEASE OF DISSOLVED ORGANIC CARBON BY PLANT TISSUES AND SOILS

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Soil and plant tissues were used to examine the effect on the release of dissolved organic carbon (DOC) of rinsing over time at two temperatures and under oxic and anoxic conditions in a laboratory incubation. The release of DOC over 60 days of incubation ranged from 0.5 to 189 mg DOC g^{-1} oven-dry material and was correlated inversely with the degree of decomposition of the material: fresh maple leaves > old maple leaves > *Sphagnum* moss > fibric peat > hemic peat = sapric peat > Inceptisol A horizon. Rates of DOC release were similar through the duration of the experiment, except for the fresh maple leaves, where release rates fell after 3 day. Rinsing, by the replacement of water in the incubating samples after 20 day, produced slower rates of DOC release, except in the Inceptisol A and sapric peat samples. There was no significant difference between DOC release under oxic and anoxic conditions, except for the Inceptisol A soil, where DOC release was greater under anoxic than under oxic conditions. The rate of DOC release at 22 °C was an average of 2.4 times greater than at 4 °C, translating into Q_{10} values of about 1.6. At 22 °C under oxic conditions, DOC production accounted for 14 to 58% (average 24%) of the total C released as DOC + CO_2, with the highest proportion in the maple leaves. Under anoxic conditions, DOC production accounted for 63 to 95% (average 82%) of the total C released as DOC + CO_2 + CH_4. Production of CH_4 under anoxic conditions was minor, accounting for <1% of the total C released. Under oxic conditions at 22 °C, the incubations released between 2 and 107% of the organic C contained in the samples, the largest proportion of which was released from the plant tissues. Microbial utilization of DOC meant that some C was double-counted, both as DOC and as subsequently emitted CO_2. Under anoxic conditions, 0.0 to 49% of the sample organic C was mineralized. The release of DOC represents the balance between production, adsorption, and desorption and microbial utilization. This release differs clearly among samples and among treatment effects. (Soil Science 2001;166:38–47)

Key words: Dissolved organic carbon, organic matter, carbon dioxide, oxic, anoxic, temperature

DISSOLVED organic carbon (DOC) is a mixture of organic compounds ranging from simple, short-chain to complex humic substances. DOC is important in soils and freshwater systems through its influence on acidity, microbial activity, nutrient availability and mobility, and effect on the toxicity and transport of metals (Thurman, 1985). Concentrations of DOC generally increase from 2 to 3 mg L^{-1} in precipitation to 10 to 50 mg L^{-1} in water passing through vegetation canopies, such as forests, and in porewater of organic soils horizons (Dalva and Moore, 1991). In mineral soil profiles, DOC concentrations generally decrease with depth. The DOC concentration in streams ranges from 2 to over 50 mg L^{-1}. The controls on DOC sorption by soil horizons are reasonably well established: laboratory and field experiments have shown that extractable

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iron and aluminum, clay mineralogy and organic carbon are the primary controls on DOC sorption in mineral soils (McDowell and Wood, 1984; Moore et al., 1992; Kaiser et al., 1996; Kaiser and Zech, 1998). Differences in concentration and flux of DOC reflect the relative rates of DOC production, sorption and consumption in systems, as well as the pathways whereby water moves DOC through ecosystems and soils.

Relatively little is known about what determines the ability of plant tissues and soil organic horizons to release DOC. The literature contains many studies that have observed an increase in DOC as water passes through the vegetation or soil organic horizons (Cronan and Aiken, 1985; Moore, 1989; Moore and Jackson, 1989; Marin et al., 1990; Dalva and Moore, 1991; Qualls and Haines, 1991; Koprivnjak and Moore, 1992; Dosskey and Bertsch, 1994). Although there are often strong spatial and temporal variations in the DOC concentration and flux within and between ecosystems, the experimental conditions are too poorly controlled to be able to identify the major factors influencing DOC production.

Christ and David (1996a) determined through laboratory incubations that increases in temperature and moisture content increased the rate of DOC production from the organic horizons of red spruce Spodosols, and they also examined the entrained and adsorbed reservoirs from which the DOC was released (Christ and David, 1996b). Gödde et al. (1996) established that DOC production rates from red spruce forest floors increased with frequency of leaching, rising temperature, and increasing C:N ratio; there was, however, no significant relationship between DOC and CO_2 production among the eight samples tested. Andersson et al. (2000) showed that temperature and pH (raised by liming) influenced the leaching of DOC from a forest mor humus in Sweden. Currie and Aber (1997) developed a model of DOC leaching from montane temperate forest floors based on a partitioning of mass loss between DOC and CO_2. The proportion lost as DOC was based on litter type (hardwood vs. coniferous) and organic composition, with the proportion of mass loss ascribed to DOC ranging from 0 to 0.74, resulting in estimated annual fluxes of 22 to 40 g DOC m^{-2}.

Although they have a common origin in soluble plant materials, the oxidation of soil organic matter, and microbial metabolites (DeLuca and Keeney, 1993; Guggenberger et al., 1994), DOC and CO_2 production may be controlled by different processes and organic matter chemistry (Gödde et al., 1996). Thus, the relative importance of DOC and CO_2 as the end-product of decomposition will depend on the type of organic matter and environmental controls.

In this study, we used a laboratory incubation technique to evaluate the effect of type of plant tissue or soil, temperature, rinsing, and oxic or anoxic conditions on the release of DOC. We examined the patterns of release of DOC into solution from three plant tissues and four soil samples at 4 and 22 °C. Rinsing simulated leaching through the replacement of the solution after day 20 and repeating the measurements for two more 20-day cycles. By combining measurements of DOC release and CO_2 and CH_4 production from the incubating samples, we also determined the effect of these conditions on the fate of the C mineralized from the samples. We hypothesized that DOC production rates would be greater in fresh than in well decomposed samples, be greater under warm than cold conditions, and be greater under oxic than anoxic conditions.

MATERIALS AND METHODS

Samples

Samples of soil and plant tissue were collected from two sites in southern Québec in early summer. At Mont St. Hilaire, 35 km east of Montreal, samples of fresh and old (over-wintered) sugar maple (*Acer saccharum*) leaves and the A horizon of a Dystrochrept were collected, as well as the surface layer (0–30-cm depth) of an adjacent swamp peat (Hemist). Maple and other deciduous species such as *Betula alleghaniensis* and *Fagus grandifolia* provide the dominant source of organic matter input into these two soils. At a bog peatland (Fibrist) near Mirabel, 50 km north of Montreal, samples were collected of the moss layer (a mixture of *Sphagnum fuscum* and *Sphagnum magellanicum,* the dominant vegetation),as well as a fibric peat sample from a depth of 15 to 30 cm and a sapric peat sample from a depth of 30 to 60 cm. The samples were stored at 4 °C until the experiment began. The pH (in H_2O) ranged from 4.5 to 5.4 in the maple leaves and the Inceptisol sample and from 3.9 to 4.8 in the *Sphagnum* and peat samples. Organic C contents were high (40–45%) in the plant tissues and peat samples, and the Inceptisol sample contained 4% org. C. Degree of decomposition ranged from none in the fresh maple leaves and *Sphagnum* moss to partial in the old maple leaves and fibric

and hemic peat samples to almost full in the sapric peat and Inceptisol samples.

Methods

Four-centimeter-thick samples of the seven types of soil and tissue were placed in acid-washed 13 × 13 × 8-m plastic containers. Intact soil samples were used to minimize disturbance. Oven-dry mass of the samples in each container ranged from 2 to 6 g for the maple leaves, 4 g for the *Sphagnum,* 5 to 20 g for the peat samples, and 100 g for the Inceptisol. One container contained water as a blank. The samples were saturated with 0.2 to 0.5 L water, leaving about half of the container free as headspace. Each sample was quickly rinsed 4 to 5 times with water to reduce, as much as possible, the DOC content of the pore water at the start of the incubation. The water from the final rinse was taken as the initial pore water and analyzed for DOC. There were three factors to examine: the effects of rinsing, temperature (4 and 22 °C), and oxidation status (oxic and anoxic) on rates of DOC production. Triplicate samples of each soil and tissue type were employed in each treatment.

After 20 days, the samples were drained, rewashed with water, the water replaced and the incubation repeated twice, resulting in measurements of DOC production in parts 1 (0 to 20 days), 2 (20 to 40 days), and 3 (40 to 60 days). This allowed a quantification of the amount of DOC lost through sequential leaching.

Samples were incubated at 4 and 22 °C to evaluate the effect of temperature. To examine the effect of oxic and anoxic conditions, half of the containers were loosely capped to ensure that aerobism was maintained and to reduce evaporation. We did not measure Eh or pO_2, but the ratio of CO_2 released under the oxic and anoxic treaments (averaging 22:1) suggests that the samples under oxic conditions were at least partially oxic. Furthermore, studies of O_2 penetration into saturated peat cores incubated under similar conditions show that at depths of 3 to 4 cm, O_2 concentrations are generally greater than 2 ppm (Blodau, pers. comm.). To create anoxic conditions, the other half of the containers were sealed with the cap, fitted with a SubaSeal septum, and flushed with N_2 for 4 to 5 h to remove O_2 from the headspace and most of the porewater.

Water samples were withdrawn on alternate days for the 4 °C treatment. Sampling was daily for the first week, and then on alternate days, for the 22 °C treatment, in anticipation of faster changes in DOC and gas exchange. This procedure was followed for parts 1 and 2, with samples taken on alternate days in all treatments in part 3. Water samples were taken with a 20-L syringe, filtered through Gelman AE 0.45 μm glass fiber paper, and an equivalent volume of distilled water was replaced in the container.

Water samples were analyzed for pH on a Fisher Accumet pH meter (model 210). DOC concentrations were determined using a Shimadzu TOC-5050 Total Organic Carbon Analyzer, which employs high temperature (680 °C) catalytic combustion. Standards were prepared from potassium biphthalate in concentrations from 0 to 1000 mg L^{-1}. The DOC concentration data were corrected for dilution and evaporation and expressed as DOC g^{-1} oven-dry soil or plant tissue, determined by oven-drying the samples at the end of the experiment.

Headspace gas samples were obtained at the same time as solution collection for DOC, analysis of carbon dioxide (CO_2) and methane (CH_4). In the anoxic treatments, gas samples were withdrawn through the septum of the continually-sealed containers. In the oxic treaments, the containers were capped, an initial sample of headspace gas was taken and another after 2 h. At each sampling date, 0.8 mL of air was withdrawn for CH_4 and 1.0 mL for CO_2 analysis.

Concentrations of CH_4 and CO_2 were determined on a Shimadzu Mini-2 gas chromatograph with a Flame Ionization Detector and a methanizer, to convert CO_2 to CH_4. N_2 was used as the carrier gas for the FID at a flow rate of 30 to 40 mL min^{-1}, with a Porapak Q 80/100 mesh column at 45 °C and an Injector/Detector temperature of 90 °C. The methanizer used Ni-reduced shimalite to reduce CO_2 to CH_4 at a detector block temperature of 385 °C using He and H_2 as the carrier gases. Gas standards of 2.57, 200, and 2000 ppmv CH_4, and 353, 2000, and 10000 ppmv CO_2 were used.

Total CO_2 produced was calculated as the sum of headspace CO_2, aqueous CO_2 using Henry's Law, and H_2CO_3 between pH 6 and 7, expressed in mg CO_2 g^{-1} oven-dry soil or plant tissue. For the samples incubated under oxic conditions, this was based on the changes in headspace CO_2 concentration during the container closure, whereas for the anoxically incubated samples, the change in CO_2 was cumulative. Production of CH_4 under anoxic conditions was based on the cumulative changes in headspace CH_4 concentration.

At the end of part 3, the soil and tissue samples were drained, oven-dried at 80 °C, and

weighed to obtain the dry mass of soil or plant tissue in each of the containers.

RESULTS

The temporal patterns of the cumulative release of DOC and CO_2 from four representative samples at 22 °C are presented in Figs. 1 and 2. There was a rapid initial increase over the first 3 days in DOC concentration within porewater of the fresh maple leaves (60 to 80 mg DOC g^{-1} d^{-1}), under both oxic and anoxic conditions, after which there was little further increase (Fig. 1). Little DOC (<1 mg DOC g^{-1} d^{-1}) was released from the fresh maple leaves in the second and third parts after replacing the original water. Rates of CO_2 emission remained steady (6 mg CO_2-C g^{-1} d^{-1}) under oxic conditions in the first part, a pattern repeated, at much lower rates (1 to 2 mg CO_2-C g^{-1} d^{-1}) during the second and third parts. After initial emission, CO_2 production rates remained very small (0.2 mg CO_2-C g^{-1} d^{-1}) under anoxic conditions in all three parts of the fresh maple leaves incubation.

In contrast to the fresh maple leaves, the *Sphagnum* moss tissues released DOC at a slower but more constant rate (0.1 mg DOC g^{-1} d^{-1}) under oxic and anoxic conditions, although less DOC was released in the second and third parts of the incubation (Fig. 1). Aerobic CO_2 emission rates from the *Sphagnum* averaged 6 mg CO_2-C g^{-1} d^{-1} in the first part and declined slightly in the second and third parts. Comparison of the release rates of DOC among the three parts of the experiment showed a significant decrease between parts 1 and 2 and 3 for the fresh maple leaves, suggesting that the reservoir of DOC in this tissue is rapidly depleted in the first part (Table 1). This pattern was less pronounced for the *Sphagnum* sample, and the old maple leaves followed a pattern intermediate between the fresh maple leaves and the *Sphagnum* moss. The same temporal relationships of DOC release occurred at 4 °C but are not reported here.

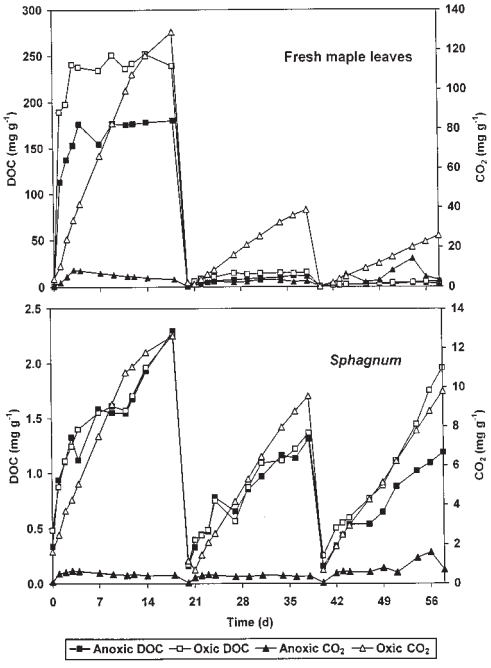

Fig. 1. Patterns of DOC and CO_2 production in samples of fresh maple leaves and *Sphagnum* incubated under oxic and anoxic conditions at 22 °C. Note variable scale of y axes.

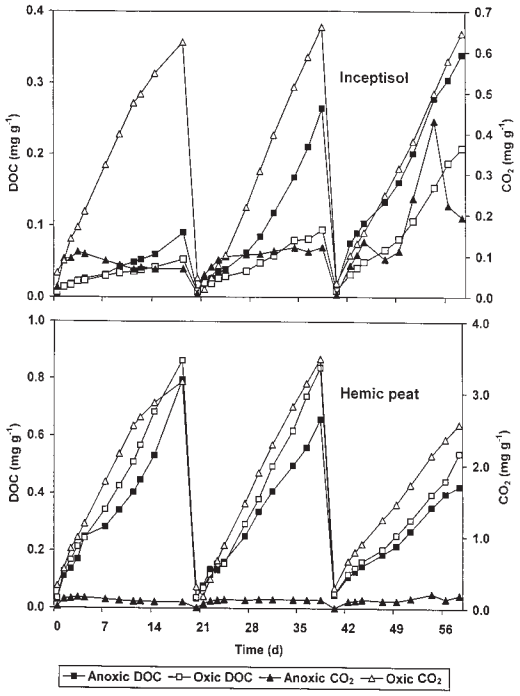

Fig. 2. Patterns of DOC and CO_2 production in samples of Inceptisol A and hemic peat soil samples incubated under oxic and anoxic conditions at 22 °C. Note variable scale of y axes.

The temporal pattern of DOC release for the soil samples was different, illustrated in Fig. 2 for the Inceptisol and hemic peat samples. Rates of DOC release from the Inceptisol were small (<0.04 mg DOC g^{-1} d^{-1}) but increased from the first to third parts to averages of 0.08 and 0.12 mg DOC g^{-1} d^{-1} under both oxic and anoxic conditions at 22 °C; this pattern was much less

TABLE 1

Quotient of the amount of DOC produced in Parts 2 and 3 of the incubation, compared with Part 1

Sample	Part	22 °C		4 °C		Mean
		Oxic	Anoxic	Oxic	Anoxic	
Fresh maple leaves	2	0.09	0.09	0.13	0.13	0.11***
	3	0.04	0.03	0.05	0.10	0.05***
Old maple leaves	2	0.28	0.26	0.46	0.45	0.38*
	3	0.18	0.21	0.54	0.57	0.38**
Inceptisol A	2	2.06	3.17	1.00	1.08	1.83
	3	4.85	4.15	1.00	1.59	2.90
Hemic peat	2	1.02	0.73	1.01	0.96	0.93
	3	0.59	0.52	0.74	0.67	0.63*
Sphagum	2	0.75	0.72	0.53	0.85	0.71*
	3	1.17	0.68	0.76	0.75	0.84
Fibric peat	2	0.61	0.94	0.18	0.67	0.67*
	3	0.64	1.02	0.33	0.67	0.66*
Sapric peat	2	1.41	0.95	0.67	0.97	1.00
	3	1.14	0.76	0.40	1.21	0.88

***, ** and * indicate significant differences from 1.00 at 0.001, 0.01 and 0.05 level, respectively, using paired *t* test.

pronounced at 4 °C (Table 1). Aerobic CO_2 emission rates from the Inceptisol were slow (0.05 mg CO_2-C g^{-1} d^{-1}) and similar among the three parts (Fig. 2). The hemic peat sample showed a slow decrease, from 0.04 to 0.025 mg DOC g^{-1} d^{-1}, in DOC release through parts 1 through 3, and aerobic CO_2 emission rates also declined in part 3 (Fig. 2). This pattern of a slow decrease in DOC release through leaching also occurred in the fibric and sapric peat samples (Table 1).

The amount of DOC released during the experiment ranged from 0.2 to 260 mg DOC g^{-1} (Table 2), with an overall ranking among samples of

fresh maple leaves > old maple leaves > *Sphagnum* moss > fibric peat hemic peat = sapric peat > Inceptisol

This pattern is the same as the degree of decomposition of the samples, from fresh plant tissues to well-humified soil organic matter.

The influence of oxic and anoxic conditions on DOC release from the seven samples is shown by the data in Table 2 and expressed as quotients

TABLE 2

Release of DOC (mg g^{-1}) from samples over 60 days of incubation combining Parts 1, 2, and 3 under oxic and anoxic conditions at 4 and 22 °C

Sample	Treatment				Mean
	22 °C		4 °C		
	Oxic	Anoxic	Oxic	Anoxic	
Fresh maple leaves	260.0	195.2	153.7	148.2	189.3
	(17.4)	(16.5)	(13.9)	(15.1)	
Old maple leaves	21.1	21.4	7.7	11.7	15.5
	(4.1)	(3.8)	(1.2)	(3.1)	
Inceptisol A	0.35	0.69	0.25	0.16	0.4
	(0.09)	(0.03)	(0.07)	(0.10)	
Hemic peat	2.24	1.89	0.62	0.60	1.3
	(0.16)	(0.23)	(0.03)	(0.08)	
Sphagnum	5.59	4.79	1.93	2.25	3.6
	(0.28)	(0.46)	(0.48)	(0.42)	
Fibric peat	2.86	2.76	1.13	1.07	2.0
	(0.25)	(0.22)	(0.26)	(0.06)	
Sapric peat	1.79	1.69	0.69	0.93	1.3
	(0.19)	(0.18)	(0.07)	(0.18)	

Figures in parentheses indicate the standard deviation of the triplicate samples used in each treatment.

for each sample and temperature treatment in Table 3. At both 22 and 4 °C, there was no overall significant difference between DOC release rates under oxic and anoxic conditions. Some treatments did show significant differences, such as fresh maple leaves at 22 °C (oxic > anoxic) and the Inceptisol at 22 °C (oxic < anoxic) and at 4 °C (oxic > anoxic).

The influence of temperature on DOC release can be assessed from the quotients of 22:4 °C rates in Table 3. This quotient was small (0.8 to 1.1) for the fresh maple leaves, but it averaged 2.6 for both the oxic and anoxic treatments of the other samples. These quotients translate into an overall Q_{10} value (between 4 and 22 °C) of 1.6, excluding the fresh maple leaves.

A summary of the three factor effects (rinsing, oxic or anoxic conditions, and temperature) on DOC release from all samples is shown in Fig. 3 and has been subjected to an Analysis of Variance (Table 4). For each factor effect, expressed as the DOC production quotient, there are large variations, indicating the complexity of the processes leading to DOC release from this wide range in organic matter and experimental conditions (Fig. 3). The overall pattern (Table 4), however, is a decrease in DOC production through rinsing ($P < 0.01$ in all samples but the sapric peat), little effect of oxic/anoxic conditions ($P < 0.01$ in Inceptisol A and hemic peat samples), and an increase in response to temperatures raised from 4 to 22 °C ($P < 0.01$ in all but the fresh maple leaves). The difference among the seven samples was significant at $P < 0.01$.

Separation of the C mobilization into DOC, CO_2, and CH_4 for the seven samples at 22 °C is shown in Table 5. Under oxic conditions, the amount of DOC released from the samples ranged from 0.4 to 260 mg g^{-1}, and the CO_2 emitted ranged from 2 to 192 mg CO_2-C g^{-1}. The division between these forms varied greatly among the samples. Although 1.4 times more DOC than CO_2-C was released from the fresh maple leaves, there was between 4.1 and 6.3 times as much CO_2-C as DOC released from the five soil samples. The old maple leaves released about 2.5 times as much CO_2-C as DOC. When the DOC and CO_2-C release rates are combined, the percentage of the sample C released over the 60-day incubation period ranged from 2% for the humic peat to 107% for the fresh maple leaves. This latter figure suggests there is some "double-counting" of C among DOC and CO_2. Where the DOC is labile, such as in the fresh maple leaves, its release from the organic matter will initially be recorded as DOC, but over the 20- day incubation period, much of this DOC may be utilized by microbes and converted to CO_2, and thus be measured twice. As the samples were incubated in the dark, there is little chance that atmospheric CO_2 could be incorporated in the sample or solution.

Under anoxic conditions, DOC release ranged from 0.7 to 195 mg g^{-1}, whereas the CO_2 produced ranged from only 0.1 to 12.8 mg CO_2-C g^{-1} (Table 4). Production of CH_4 was an insignificant part of the C budget, apart from the old maple leaves, which, lying on the forest floor, may have had an active methanogenic population. In all samples incubated anaerobically, DOC release rates were larger than CO_2-C production rates by factors ranging from 2 (in the old maple leaves) through 3 to 8 in the peat and *Sphagnum* samples, to 19 in the fresh maple leaves. Although some CO_2 was produced intially in the anaerobic incubations, little further production occurred after 4 or 5 days. The amount of C released as DOC, CO_2, and CH_4 during the incubation ranged from 1 to 49% of the original sample C, an average of 25% of that released in the aerobic incubations. Some indication of the influence of anoxic conditions on CO_2 production is revealed by oxic:anoxic CO_2 production quotients

TABLE 3

Quotient of DOC release under oxic and anoxic conditions at 4 °C and 22 °C over 60 days

Sample	Treatment			
	22 °C oxic:anoxic	4 °C oxic:anoxic	Oxic 22:4	Anoxic 22:4
Fresh maple leaves	1.33	1.04	1.69	1.32
Old maple leaves	0.99	0.66	2.75	1.83
Inceptisol A	0.51	1.55	1.40	4.31
Hemic peat	1.19	1.03	3.61	3.12
Sphagnum	1.17	0.86	2.89	2.13
Fibric peat	1.04	1.06	2.53	2.58
Sapric peat	1.06	0.74	2.59	1.82

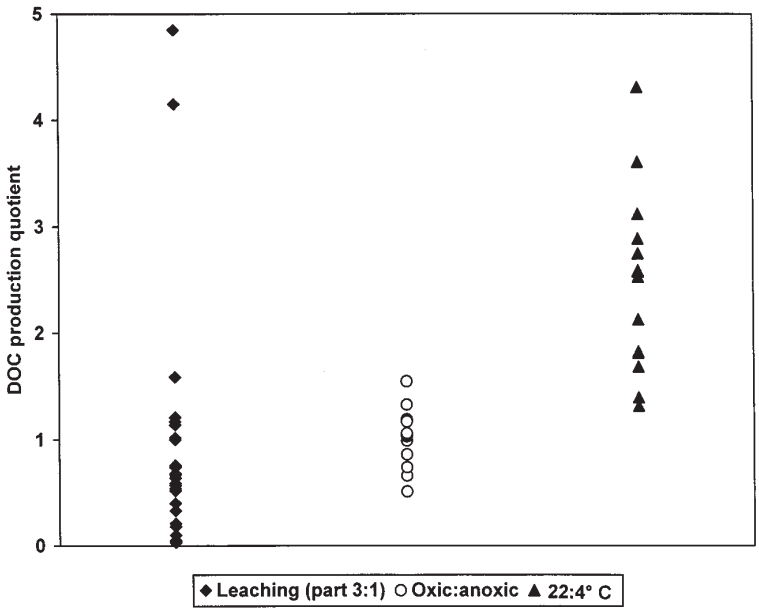

Fig. 3. Graphical summary of the importance of leaching, oxic/anoxic conditions and temperature on DOC release. Each point represents one sample, expressed as the ratio between parts 3 and 1, oxic and anoxic, and 22 and 4 °C treatments.

at 22 °C ranging from 4 in the old maple leaves to 16 to 35 for the other samples.

DISCUSSION

The DOC release rates presented here are net rates and represent the balance between the release of DOC from organic matter, its exchange and sorption on particle surfaces, its incorporation into microbial tissue, and its release as CO_2 and CH_4 through decomposition. Assessments of the bioavailability of DOC in soils are few (e.g., Boyer and Groffman, 1996; Qualls and Haines, 1992; Yano et al., 1998) though the lability of DOC in freshwater bodies such as streams and lakes has been studied more intensively (e.g. Leff and Meyer, 1991; Søndergaard and Middelboe, 1995). Qualls and Haines (1992) reported that between 14 and 33% of the DOC released in a deciduous forest was metabolized over 134 days, with most metabolism occurring in the first 20 days. Relative DOC biodegradability decreased from throughfall and forest floor to B and A horizons; a deciduous leaf leachate sample showed the highest biodegradation rate, 45% in 20 days

TABLE 4

Results of Analysis of Variance summarizing differences in rates of DOC production within and among samples under varying factors of rinsing, oxic-anoxic conditions and temperature. Differences among sample types as identified under the combined category. For each sample, n = 36

Sample	Factor							
	Rinsing		Oxic-anoxic		Temperature		Type	
	F-ratio	*P*	F-ratio	*P*	F-ratio	*P*	F-ratio	*P*
Fresh maple leaves	540.6	<0.001	0.5	0.501	2.7	0.115		
Old maple leaves	50.5	<0.001	0.3	0.572	63.1	<0.001		
Inceptisol A	28.2	<0.001	12.8	<0.001	101.0	<0.001		
Hemic peat	16.3	<0.001	8.3	0.008	293.5	<0.001		
Sphagnum	6.1	0.007	2.3	0.131	238.9	<0.001		
Fibric peat	18.9	<0.001	1.5	0.239	434.7	<0.001		
Sapric peat	1.4	0.257	1.6	0.224	196.0	<0.001		
Combined	587.9	<0.001	0.4	0.539	15.3	<0.001	791.8	<0.001

TABLE 5

Release of DOC, CO_2, and CH_4 from soils and plant tissues incubated over 60 days at 22 °C under oxic and anoxic conditions. Units are mg C g^{-1}, except for CH_4 which is μg CH_4^- C g^{-1}. Figures in brackets represent the combined (DOC + CO_2 + CH_4) percentage of the sample C released during the incubation

Sample	Oxic			Anoxic			
	DOC	CO_2	C released (%)	DOC	CO_2	CH_4	C released (%)
Fresh maple leaves	260.0	192.1	107	195.2	10.1	<0.1	49
Old maple leaves	21.1	53.4	19	21.4	12.8	70	9
Inceptisol A	0.4	1.7	4	0.7	0.1	0.5	6
Hemic peat	2.2	9.4	3	1.9	0.4	0.9	2
Sphagnum	5.6	33.5	9	4.8	1.5	<0.1	1
Fibric peat	2.9	18.0	5	2.8	0.6	<0.1	0.1
Sapric peat	1.8	7.3	2	1.7	0.2	<0.1	0.1

(Qualls and Haines, 1992). Boyer and Groffman (1996) reported that 10 to 25% of water-extractable soil C was biodegradable over 14 days. Of the DOC contained in rivers and lakes, 15 to 20% may be regarded as labile, or subject to microbial utilization at 15 to 20 °C under oxic conditions and for a period of about 1 week (Søndergaard and Middelboe, 1995). One can speculate that a larger proportion of the DOC released by plant tissues is labile compared with DOC released from soils (Qualls and Haines, 1992). DOC production rates reported in this paper are minimum values. Under oxic conditions, and particularly for the plant tissue samples, a significant proportion of the DOC released by the samples was probably utilized microbially, either released as CO_2 (leading to a double-counting of C) or incorporated into microbial tissue during the incubation.

Guggenberger et al. (1994) examined the origin of DOC and its pathways of mobilization in spruce forest floors and concluded that the complex mixture of DOC represents a combination of plant-derived and microbial metabolite products. They proposed that the hydrophobic and hydrophilic acid and neutral fractions contained different compounds relating to their plant or microbial origin. DOC can be released through the leaching of organic matter and plant tissues or the product of microbial degradation of soil organic matter. In spruce forest floors, Christ and David (1996b) recognized entrained and adsorbed DOC phases, which were released by leaching and replenished by production (dominantly hydrophobic fractions) and microbial activities (dominantly hydrophilic fractions). They noted that the build-up of high DOC concentrations could inhibit the release of DOC, particularly the hydrophobic fractions. Qualls and Haines (1992) also ascribed much of the variation in DOC concentrations in soils to processes of adsorption.

There was little evidence in the present study for the inhibition of DOC release through the buildup of large DOC concentrations in porewater; this may be because the incubations were conducted for only 20 days, after which the water was replaced. Christ and David (1996b) observed much greater rates of DOC production in spruce forest floors when the leaching was frequent (once per day compared with once per week). The differences in DOC production among the three phases of the experiment suggest that the mechanisms of DOC production, microbial solubilization and leaching, vary among the substrate types and experimental conditions. Clearly important in controlling DOC production is the type of substrate, especially its chemical composition and degree of decomposition, with smaller amounts of DOC released from better decomposed materials. Working with eight red spruce forest floors, Gödde et al. (1996) observed a positive correlation between the amount of DOC released and the C:N ratio of the sample, which may relate to degree of decomposition.

The production of DOC showed a more limited response to increasing temperature than CO_2 production. In this study, the Q_{10} value for DOC production over the range 4 to 22 °C averaged 1.6. In studies of DOC release from forest floors, Christ and David (1996a) and Gödde et al. (1996) reported Q_{10} values ranging from 1.5 to 2.0. These temperature responses of DOC production are smaller than is commonly observed for CO_2 release from soils. Emission of CO_2 was not measured at 4 °C in the present study, but Gödde et al. (1996) observed Q_{10} values for CO_2 emission from forest floors of 2.6 to 3.3, over the temperature range of 3 to 20 °C, and Kirschbaum

(1995) noted that Q_{10} values decrease as temperature increases, from about 4.5 at 10 °C to 2.5 at 20 °C. Boone et al. (1998) recently presented data that suggested the Q_{10} values for soil respiration in profiles lacking roots was 2.5, whereas this value rose to 4.6 for root respiration and rhizosphere decomposition.

The weaker response of DOC release to temperature, compared with CO_2 emission, may be related to the involvement of DOC production with both microbial enzymatic activity and physical leaching of the material, the latter being less sensitive to temperature change. The limited temperature response of DOC release from the fresh maple leaves, in which leaching is probably the dominant process of DOC release, supports this contention. Furthermore, the study determined net DOC production, a function of DOC release and microbial consumption, and the combination of these processes may reduce the overall sensitivity to temperature further. Although there was no variation in water content in the present study (all samples were saturated), Christ and David (1996a) and Gödde et al. (1996) showed that both increasing soil moisture content and more frequent leaching increased the rate of DOC production. Thus, warmer and wetter environments increase rates of DOC production.

The observation that DOC production was similar under oxic and anoxic conditions was unexpected. If much of the release of DOC is related to microbial activity, then one would have anticipated lower DOC production rates under anoxic conditions, as was clearly observed for CO_2 production. Under oxic conditions, however, some of the DOC produced may have been consumed by microbes, lowering the observed net DOC production rate, which may, in part, have caused this condition. DOC lability would be much smaller under anoxic conditions compared with oxic conditions. The cool, wet, anoxic conditions found in peatlands may thus be the ideal conditions for DOC production and may account for the high DOC concentrations found commonly in peat porewaters.

Caution should be exercised, however, in translating the absolute DOC production rates observed in this laboratory incubation to field conditions. For example, peat profiles contain about 100 kg organic matter m^{-2} in the top meter of the profile. Assuming that much of the profile is cool and anoxic, the results of this study suggest that the peat would produce between 1 and 2 mg DOC g^{-1} over 60 days. This translates into total DOC production in the profile of between 200 and 400 g m^{-2} over a 120-day season. DOC export from catchments dominated by peatlands rarely exceeds 50 g m^{-2} yr^{-1} (Moore, 1997). Clearly, there must be less DOC produced under field conditions, or processes affecting DOC production such as inhibition, adsorption, or microbial utilization reduce the net production rate to the observed export rate of peatlands.

The results of this study suggest that there may be a general relationship in the partitioning of C mobilized as DOC and CO_2 under oxic and anoxic conditions (Fig. 4). The higher the DOC production rate under oxic conditions, the smaller the ratio of CO_2 to DOC production. The eight red spruce forest floors incubated by Gödde et al. (1996) also follow this pattern, when corrected to 20 °C, falling between the values of DOC and CO_2 production observed in the fresh and old maple leaves. In their model of DOC leaching from forest floors, compared with field measurements, Currie and Aber (1997) ascribed the highest proportion of C loss as DOC (compared with CO_2) to the least decomposed materials (e.g. lignocellulose and unprotected cellulose fractions), and confirmed the importance of substrate chemistry and degree of decomposition on CO_2 and

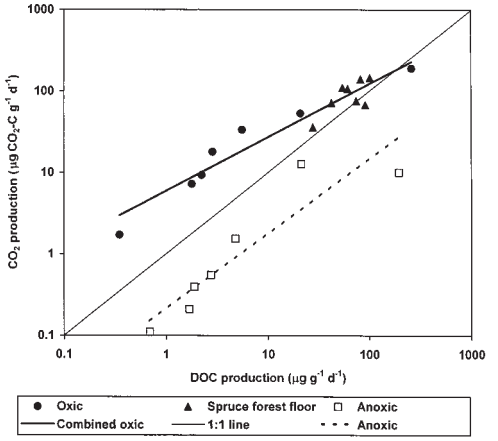

Fig. 4. The partitioning of mobilized C between DOC and CO_2 during the oxic and anoxic incubations at 22 °C reported here, and oxic incubations of eight red spruce forest floors at 10 °C, corrected to 20 °C, reported by Gödde et al. (1996). The upper line represents the regression between CO_2 and DOC production for the 15 oxic incubations: $\log_{10}CO_2 = 0.576(\pm 0.121) + 0.758(\pm 0.079)\log_{10}DOC$, $r^2 = 0.875$. The middle line represents the 1:1 relationship. The lower line represents the regression for the seven anoxic incubations: $\log_{10}CO_2 = -0.647(\pm 0.183) + 0.890(\pm 0.173)\log_{10}DOC$, $r^2 = 0.841$.

DOC production rates. These relationships of DOC and CO_2 production from decomposing soil materials deserve further investigation.

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REFERENCES

Andersson, S., S. I. Nilsson, and P. Saetre. 2000. Leaching of dissolved organic carbon (DOC) and dissolved organic nitrogen (DON) in mor humus as affected by temperature and pH. Soil Biol. Biochem. 32:1–10.

Boone, R. D., K. J. Nadelhoffer, J. D. Canary, and J. P. Kaye. 1998. Roots exert a strong influence on the temperature sensitivity of soil respiration. Nature 396:570–572.

Boyer, J. N., and P. M. Groffman. 1996. Bioavailability of water extractable organic carbon fractions in forest and agricultural soil profiles. Soil Biol. Biochem. 28:783–790.

Christ, M., and M. B. David. 1996a. Temperature and moisture effects on the production of dissolved organic carbon in a Spodosol. Soil Biol. Biochem. 28:1191–1199.

Christ, M., and M. B. David. 1996b. Dynamics of extractable organic carbon in Spodosol forest floors. Soil Biol. Biochem. 28:1171–1179.

Cronan, C. S., and G. R. Aiken. 1985. Chemistry and transport of soluble humic substances in forested watersheds of the Adirondack Park, New York. Geochim. Cosmochim. Acta 49:1697–1705.

Currie, W. S., and J. D. Aber. 1997. Modeling leaching as a decomposition process in humid montane forests. Ecology 78:1844–1860.

Dalva, M., and T. R. Moore. 1991. Sources and sinks of dissolved organic carbon in a forested swamp catchment. Biogeochemistry 15:1–19.

DeLuca, T. H., and D. R. Keeney. 1993. Soluble anthrone-reactive carbon in soils: Effect of carbon and nitrogen amendments. Soil Sci. Soc. Am. J. 57: 1296–1300.

Dosskey, M. G., and P. M. Bertsch. 1994. Forest sources and pathways of organic matter transport to a blackwater stream: A hydrologic approach. Biogeochemistry 24:1–19.

Gödde, M., M. B. David, M. Christ, M. Kaupenjohann, and G. F. Vance. 1996. Carbon mobilization from the forest floor under red spruce in the northeastern U.S.A. Soil Biol. Biochem. 28:1181–1189.

Guggenberger, G., W. Zech, and H.-F. Schulten. 1994. Formation and mobilization pathways of dissolved organic matter: evidence from chemical structure studies or organic matter fractions in acid forest floor solutions. Org. Geochem. 21:51–66.

Kaiser, K., G. Guggenberger, and W. Zech. 1996. Sorption of DOM and DOM fractions to forest soils. Geoderma 74:281–303.

Kaiser, K., and W. Zech. 1998. Rates of dissolved organic matter release and sorption in forest soils. Soil Sci. 163:714–725.

Kirschbaum, M. U. E. 1995. The temperature dependence of soil organic matter decomposition and the effect of global warming on soil organic C storage. Soil Biol. Biochem. 27:753–760.

Koprivnjak, J-F., and T. R. Moore. 1992. Sources, sinks and fluxes of dissolved organic carbon in subarctic fen catchments. Arct. Alp. Res. 24:204–210.

Leff, L. G., and J. L. Meyer. 1991. Biological availability of dissolved organic carbon along the Ogeechee River. Limnol. Oceanogr. 36:315–323.

Marin, L. E., T. K. Kratz, and C. J. Bowser. 1990. Spatial and temporal patterns in the hydrogeochemistry of a poor fen in northern Wisconsin. Biogeochemistry 11:63–76.

McDowell, W. H., and T. Wood. 1984. Podzolization: Soil processes control dissolved organic carbon concentrations in stream water. Soil Sci. 137:13–32.

Moore, T. R. 1989. Concentrations, fluxes and characteristics of dissolved organic carbon in forested and disturbed catchments, Westland, New Zealand. I. Maimai. Water Resour. Res. 25:1321–1330.

Moore, T. R. 1997. Dissolved organic carbon: Sources, sinks and fluxes and role in the soil carbon cycle. *In* Soil Processes and the Carbon Cycle. R. Lal, J.M. Kimble, R.F. Follett, and B.A. Stewart (eds.). CRC Press, Boca Raton, FL, pp. 281–292.

Moore, T. R., and R. J. Jackson. 1989. Concentrations, fluxes and characteristics of dissolved organic carbon in forested and disturbed catchments, Westland, New Zealand. II. Larry River. Water Resour. Res. 25:1331–1339.

Moore, T. R., W. de Souza, and J-F. Koprivnjak. 1992. Controls on the sorption of dissolved organic carbon by soils. Soil Sci. 154:120–129.

Qualls, R. G., and B. L. Haines. 1991. Geochemistry of dissolved organic nutrients in water percolating through a forest ecosystem. Soil Sci. Soc. Am. J. 55:1112–1123.

Qualls, R. G., and B. L. Haines. 1992. Biodegradability of dissolved organic matter in forest throughfall, soil solution, and stream water. Soil Sci. Soc. Am. J. 56:578–586.

Søndergaard, M., and M. Middelboe. 1995. A cross-system analysis of labile dissolved organic carbon. Mar. Ecol. Prog. Ser. 118:283–294.

Thurman, E. M. 1985. Organic Geochemistry of Natural Waters. M. Nijhoff/W. Junk Publishers, Boston.

Yano, Y., W. H. McDowell, and N. E. Kinner. 1998. Quantification of biodegradable dissolved organic carbon in soil solution with flow-through bioreactors. Soil Sci. Soc. Am. J. 62: 1556–1564.