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Controls on the release of dissolved organic carbon and nitrogen from a deciduous forest floor investigated by manipulations of aboveground litter inputs and water flux

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Abstract. Although dissolved organic matter (DOM) released from the forest floor plays a crucial role in transporting carbon and major nutrients through the soil profile, its formation and responses to changing litter inputs are only partially understood. To gain insights into the controlling mechanisms of DOM release from the forest floor, we investigated responses of the concentrations and fluxes of dissolved organic carbon (DOC) and nitrogen (DON) in forest floor leachates to manipulations of throughfall (TF) flow and aboveground litter inputs (litter removal, litter addition, and glucose addition) at a hardwood stand in Bavaria, Germany. Over the two-year study period, litter manipulations resulted in significant changes in C and N stocks of the uppermost organic horizon (Oi). DOC and DON losses via forest floor leaching represented 8 and 11% of annual litterfall C and N inputs at the control, respectively. The exclusion of aboveground litter inputs caused a slight decrease in DOC release from the Oi horizon but no change in the overall leaching losses of DOC and DON in forest floor leachates. In contrast, the addition of litter or glucose increased the release of DOC and DON either from the Oi or from the lower horizons (Oe + Oa). Net releases of DOC from the Oe + Oa horizons over the entire manipulation period were not related to changes in microbial activity (measured as rates of basal and substrate-induced respiration) but to the original forest floor depths prior to manipulation, pointing to the flux control by the size of source pools rather than a straightforward relationship between microbial activity and DOM production. In response to doubled TF fluxes, net increases in DOM fluxes occurred in the lower forest floor, indicating the presence of substantial pools of potentially soluble organic matter in the Oe + Oa horizons. In contrast to the general assumption of DOM as a leaching product from recent litter, our results suggest that DOM in forest floor leachates is derived from both newly added litter and older organic horizons through complex interactions between microbial production and consumption and hydrologic transport.

Introduction

Dissolved organic matter (DOM) in soil solution represents one of the most mobile and actively cycling fractions among soil organic matter pools (Ellert and Gregorich 1995; Zsolnay 1996). Despite continuous production and consumption in all horizons of the soil profile, the largest net production of DOM generally occurs in the forest floor (Sollins and McCorison 1981; Cronan and Aiken 1985;

McDowell and Likens 1988; Michalzik et al. 2001). DOM released from the forest floor has been recognized for its importance as a carrier of inorganic nutrients (Yavitt and Fahey 1986; Qualls et al. 1991; Cortina et al. 1995) and sesquioxides and metals (Dawson et al. 1978; Pohlman and McColl 1988). It also has great implications for the belowground C cycle, because the leaching loss of dissolved organic carbon (DOC) can account for a substantial portion of the annual litterfall C (McDowell and Likens 1988; Qualls et al. 1991; Hongve et al. 2000) and total forest floor C loss (Cronan 1985; Yavitt and Fahey 1986; Vance and David 1991). This leachate C loss from the forest floor has often been overlooked in determining soil C budgets, while the forest floor is receiving much attention due to its role as a temporary sink for increased litter C inputs following CO_2 enrichment (Schlesinger and Lichter 2001) or reforestation (Richter et al. 1999).

Contrasting views exist concerning major sources of DOM and the relative significance of biotic and abiotic controls on DOM release from the forest floor (Kalbitz et al. 2000; Qualls 2000; Neff and Asner 2001). Although some authors have stressed the quantitative importance of humified organic matter in forest floor DOM production (McDowell and Likens 1988; Zsolnay 1996), field experiments have reported recent litter as the primary source of DOM in forest floor leachtes (Qualls et al. 1991; Casals et al. 1995; Michalzik and Matzner 1999). Other potential sources of DOM include root exudates and biomass of soil microbes and fauna (Kalbitz et al. 2000). Some field studies have suggested that DOM production in the forest floor is largely controlled by microbial activity, based on higher DOM concentrations observed in warmer seasons (Cronan and Aiken 1985; McDowell and Likens 1988; Dai et al. 1996). A correlation between temperature and DOM production has been observed in many laboratory experiments (Christ and David 1996b; Gödde et al. 1996; Andersson et al. 2000). In addition, DOM in soil solution is characterized by lower molecular weights and higher degrees of oxidative degradation of plant-derived organic matter compared to solid organic matter, suggesting microbial production of DOM (Guggenberger et al. 1994; Dai et al. 1996; Kaiser et al. 2001). Regarding this microbial link to DOM production, there have been few attempts to examine the relationships between resource availability, microbial activity, and DOM production under field conditions. In particular, responses of microbial DOM production mechanisms to changes in litter inputs (e.g., increased litter inputs following CO_2 enrichment) are still poorly understood (King et al. 2001; Hagedorn et al. 2002).

Hydrology can also play an important role in both production and mobilization of DOM in the forest floor. The formation of water-soluble organic materials can be increased through the positive effect of moisture on microbial activity (Falkengren-Grerup and Tyler 1993) or through the rewetting effect after dry periods (Christ and David 1996b; Lundquist et al. 1999). Since substantial amounts of potentially soluble organic materials exist in an adsorbed phase (Christ and David 1996a), the amount of percolating water can play a crucial role in mobilizing DOM from different sources (Tipping et al. 1999). Increased water flow and high leaching frequency were found to increase DOM release in some laboratory leaching experiments (Christ and David 1996a; Gödde et al. 1996; Judd and Kling 2002).

Water fluxes have also been suggested to be a key driver of DOM export either from the forest floor (Michalzik et al. 2001) or the whole soil profile (Tipping et al. 1999).

Here, controls on the production and mobilization of dissolved organic nitrogen (DON) as well as DOC in the forest floor were investigated using manipulations of resource availability and throughfall (TF) flux at a European beech-dominated hardwood stand. The resource availability in the forest floor was manipulated by excluding aboveground litter inputs or amending fresh litter or glucose. During snow-free seasons, TF inputs were doubled using automatic sprinklers. Specific objectives of this study were as follows:

1. To explore the relationships between resource availability, microbial activity, and DOM production in different forest floor horizons;
2. To investigate the role of water flux in mobilizing DOM from different organic matter pools in the forest floor; and
3. To evaluate the role of DOM as a vehicle for C and N export from the forest floor and its responses to increased aboveground litter inputs.

Materials and methods

Study site and experimental setup

Manipulation plots are located at a long-term ecological research site (1.3 ha) of the Bayreuth Institute for Terrestrial Ecosystem Research (BITOEK) within the Steigerwald National Park, Bavaria, Germany (49°52′ N, 10°27′ E). The research site lies on the upper part of the 55 ha Steinkreuz watershed. Elevation of the watershed ranges from 400 to 460 m. The annual mean temperature is 7.5 °C and average precipitation approximately 75 cm year^{-1}. The site is a hardwood stand composed of European beach (*Fagus sylvatica* L.) and Sessile oak (*Quercus petraea* (Matt.) Liebl.), both approximately 130 years old. The understory vegetation is represented by scattered patches of *Deschampsia flexuosa*, *Vaccinium myrtillus*, and seedlings of dominant trees. Soils, classified as Dystric Cambisol (FAO-classification), are sandy to loamy and have developed from underlying sandstones. The forest floor contains typical moder type O horizons: distinct Oi and Oe and thin Oa. Our measurements of soil pH (soil: deionized water = 1:12, w/w) showed increasing acidity with increasing humification degrees of forest floor horizons (Oi: 5.3, Oe: 4.9, Oa: 4.4). Chemical composition of soil organic matter in all soil horizons has recently been analyzed at this site using ^{13}C CPMAS NMR spectroscopy and CuO oxidation (Rumpel et al. 2002).

Treatment plots (2 m × 2 m each, a total of 19 plots) were established in April 1999. Plots were spaced by a minimum 1-m distance. No tree boles and rare ground vegetation were present on the plots. Four plots were randomly assigned to one of the following treatments: control (normal litter inputs), no litter (exclusion of aboveground litter inputs), double litter (doubling aboveground litter inputs), and

double TF (doubling TF inputs). Amendment of glucose equivalent to the annual aboveground litter C input was made at three additional plots. Since September 1999 aboveground litter inputs have been excluded from the no litter plots by placing a roof-shaped litter trap composed of a wooden frame, cover net and side nets (2 m $\times$ 2 m) during snow-free months (from April to December). Since the cover net (pore size $<$5 mm) was evaluated to have minimal water retention by pre-installment tests (measuring percent recovery of water sprayed over the net), under normal rainfall events only small portions ($<$5%) of TF flow might have been excluded by the litter trap itself. From September to December, fresh litter taken from the no litter plots were added to the double litter plots. Glucose was applied to the glucose plots four times: October 1999 and 2000 (180 g C m^{-2} equivalent to the autumnal litterfall C); July 2000 and May 2001 (60 g C m^{-2} equivalent to the litterfall C input during the rest time of the year). The first two applications were made using aqueous glucose solution. Thereafter, glucose was amended as powder, followed by the addition of small amount of deionized water.

TF inputs were doubled in a circular area (approximately 1 m^2) within the double TF plots using an automatic sprinkling system. The sprinkler sprayed TF water collected in an adjacent TF sampler (1 m $\times$ 1 m) to the plots during rainfall. This real-time TF addition is assumed to double not only TF volumes but also inputs of all the chemical components in TF. Due to technical problems, the sprinkler functioned only partially in the beginning. Therefore, the reported results here refer only to the periods from April to December 2000 and from April to June 2001.

Zero-tension lysimeters were installed beneath the Oi and Oa horizons (one per horizon at each plot). The lysimeters, draining a surface area of 707 cm^2, consisted of a disc-shaped plastic container and a fiberglass screen. To install lysimeters below the Oi horizon, Oi material within the area of lysimeter surface size was removed at first. A lysimeter was set up in the place and then the removed Oi material was put on the lysimeter. Since the Oa horizon was not always distinct and the depth of whole organic horizons was very variable, we cut a rectangular block of forest floor, using a steel frame and a knife. The forest floor block was separated from mineral soil materials, measured for the depth at each side and firmly put on the lysimeter now placed in the hole. Sampling bottles were buried in a pit that was dug at downslope positions. During the equilibrium period (3 months after the installation), sampled forest floor leachates were analyzed only for examining disturbance effects of installation. Soil solution was also collected using ceramic suction cups buried at 20 cm depth below the forest floor (upper B horizon). Suction applied was approximately 30 kPa. Three replicates were used for all treatments.

TF was collected using 12 collectors systematically installed in an area next to the treatment plots. The 12 replicates were pooled to form four composite samples. Since the weight of litter taken from the no litter plots was measured only from September to December, the litterfall amount during the rest period of the year was obtained from 10 litter traps (1 m $\times$ 1 m) installed at the site. The sampling of aboveground litterfall included all fallen organic materials except coarse woody debris with a diameter over 1 cm. C and N contents of litter were measured for

composite samples of three litter types (foliage, woody debris, and fruit and flower parts) two or three times per year (Lischeid and Gerstberger 1997). Meteorological data were recorded at a weather station located in a clearing 100 m away from the site.

Sample collection and laboratory analyses

TF, forest floor leachate and soil solution were collected biweekly. Within 24 h after collection, solution samples were measured for pH and electrical conductivity and then filtered through a pre-rinsed (deionized water) cellulose-acetate membrane filter (0.45 μm pore size). The filtered samples were refrigerated at 2 °C prior to analysis. Generally within 2 weeks after collection, solution samples were measured for DOC, total dissolved N (TDN), NO_3-N, NH_4-N, and Cl.

DOC and TDN in filtered samples were simultaneously measured through CuO-catalyzed, high-temperature (950 °C) oxidation followed by infrared detection of CO_2 and NO_x determination using an external chemiluminescence detector (high-TOC-Analysator, Fa. Elementar, Germany). This simultaneous measurement of DOC and TDN uses the combined application of the high-temperature catalytic oxidation method for DOC determination and a commercially available chemiluminescent N detector (Chemoluminеszens-Detektor, Fa. Abimed, Germany). A similar procedure for TDN measurement is described in detail by Merriam et al. (1996). Prior to determination of total dissolved carbon (TDC), dissolved inorganic carbon (DIC) in an aliquot sample was determined by adding phosphoric acid and measuring released CO_2. DOC was determined as the difference between TDC and DIC in solution samples. We used a mixed standard solution (Na_2CO_3, trishydroxymethylaminomethane, and urea) to evaluate the accuracy of measurements of TIC, DOC, and TDN. Analytical error for both DOC (detection limit: 0.75 mg C L^{-1}) and TDN (detection limit: 0.23 mg N L^{-1}) measurements was generally below 1.5%. A standard reference material (Canadian Colored Water ION 94; 10 mg DOC L^{-1}, 0.66 mg DIC L^{-1}) was routinely measured for DOC, along with solution samples. Percentage recovery of DOC in this reference solution was within ±5% accuracy. NH_4 were measured by colorimetrical flow injection analysis (Lachat FIA, Germany; detection limit: 0.02 mg N L^{-1}; analytical error 1.5%). We measured NO_3 by ion chromatography (Dionex 2000i-SP, Germany; detection limit: 0.04 mg N L^{-1}; analytical error 1%). DON was calculated as the difference between TDN and dissolved inorganic N (DIN: NO_3-N plus NH_4-N).

To measure changes in forest floor C and N pools including microbial C and soluble organic C, forest floor samples were collected three times from all plots except double TF: October 1999, October 2000, and May 2001. All samplings were made 2 weeks after the application of glucose. At each plot, three to five forest floor cores were randomly sampled using a metal ring (inner diameter: 10 cm). Samples were transported on ice to the laboratory, where they were refrigerated at 5 °C overnight. Forest floor cores were separated into two horizons (Oi and Oe + Oa) and then pooled into one composite sample per horizon within each plot. All

following measurements were made on duplicate samples from these composite samples.

For the determination of forest floor C and N stocks, all samples were removed of macrofauna, undecomposed fruit structures (nuts and acorns), and woody debris with a diameter >1 cm by hand and then weighted prior to further sample preparation for microbial biomass measurements. An aliquot of all samples was oven-dried (65 °C) for 48 h to determine the initial moisture content. The dried samples were then ground and analyzed for total C and N contents on a CN elemental analyzer (CHN-O-Rapid, Foss Heraeus, Germany). These data of C and N contents, together with dry mass of samples, were used to calculate forest floor C and N stocks on an area basis.

To measure microbial biomass C, forest floor samples were further removed of all remaining soil fauna and other coarse materials such as undecomposed fine woody debris and live roots. Oi litter was cut into pieces (<1 cm × 1 cm) and Oe + Oa samples were sieved (5 mm). Samples were then mixed thoroughly and stored in polyethylene bags at 5 °C for a few days. Within 5 days after collection, microbial biomass C was determined by chloroform fumigation-extraction (Vance et al. 1987). Microbial C was estimated from the following relationship: microbial C = the difference in 0.5 M K_2SO_4-extractable organic C between fumigated (with chloroform in a vacuum dessicator for 24 h) and nonfumigated samples divided by a correction factor (0.45) (Vance et al. 1987; Joergensen 1996). DOC in K_2SO_4 extracts was measured by persulfate-UV-oxidation followed by infrared detection of CO_2 (Liqui TOC, Foss Heraeus, Germany). K_2SO_4-extractable organic C was also used as a measure of soluble organic C in the forest floor (Zsolnay 1996).

For the Oe + Oa samples collected in May 2001, we also measured basal respiration and substrate-induced respiration (SIR) following the methods adapted from Anderson and Domsch (1978) and Lin and Brookes (1999). Preliminary measurements showed 20 mg g^{-1} dry soil as an optimal glucose concentration that induced the highest initial respiration response. Duplicate moist samples (2 g dry weight) were placed in air-tight glass bottles (120 ml) and amended with 4 ml deionized water (for basal respiration) or glucose solution (for SIR). The samples were then incubated at 25 ± 1 °C for 3 h and the amount of CO_2 evolved in the headspace was determined by taking a 100 µl syringe sample and analyzing CO_2 concentrations using a gas chromatograph with a thermal conductivity detector (Hewlett Packard 6890, Agilent Technologies GmbH, Germany). During incubation, bottles were shaken on a mechanical shaker (150 rev min^{-1}) to prevent possible O_2 limitation that inhibits microbial respiration at high soil water contents (Lin and Brookes 1999). The average rate of CO_2 released from water or glucose added samples over the 3 h incubation was used a measure of basal respiration or SIR, respectively.

Calculations and statistical analyses

The data reported here cover a 3-month pre-treatment period and two manipulation years from October 1999 through September 2001. Fall here represents the period from October to December, when the bulk of annual aboveground litter falls.

Winter, spring, and summer cover each 3-month period from January to March, from April to June, and from July to September, respectively. To calculate average element concentrations during each season or the whole study period, biweekly concentrations were volume-weighted with measured volumes of TF, forest floor leachate, and soil solution. For the glucose plots, DOC concentration data obtained within 2 or 4 weeks after the application of glucose were not included in the calculation of seasonal average concentrations and fluxes to exclude the possibility of direct leaching of applied glucose. Concentrations below the detection limits were replaced by the half of each detection limit value and some missing values by the average value of at least two remaining replications at each treatment.

Element fluxes in TF were calculated using measured TF volumes and volume-weighted seasonal average concentrations. However, water fluxes through two forest floor horizons were estimated using an empirical relationship between the volumes of TF and forest floor leachate that was derived from a previous study conducted at the site (Solinger et al. 2001), because the volumes of collected leachates generally did not exceed 50% of TF volumes. According to the reported values by Solinger et al. (2001), who collected forest floor leachate using tension plate lysimeters with a plausible water-collection efficiency, we determined 80 and 75% of TF volumes as conservative estimates for water fluxes through Oi and Oa, respectively.

The measured leachate volumes were generally similar among treatments except for the Oa leachates collected at the no litter and double litter plots. However, based on no significant differences in Cl concentrations between treatments and TF, it is assumed that the different water-collection efficiency of each lysimeter has not significantly influenced element concentrations. Thus, the estimated values were uniformly applied for the calculation of seasonal water fluxes at all treatments including the double TF plots, the TF inputs of which were assumed to be twice those for the control. The actual proportion of collected water by Oa lysimeters in doubled TF fluxes averaged 62%. Seasonal element fluxes in forest floor leachate were calculated through multiplying volume-weighted seasonal mean concentrations by estimated water fluxes. These seasonal element fluxes were summed for obtaining 1- or 2-year fluxes.

Differences among treatments were analyzed using one-way analysis of variance (ANOVA). Prior to analysis, all data were examined for homogeneity of variance. In cases of unequal variance, data were log transformed. When significant effects were detected, pairwise comparisons between means were made with Tukey's honestly significant difference (HSD) test (SPSS Inc. 1999). Differences between means of seasonal element fluxes at the control and double litter plots were analyzed using *T*-test.

Results and discussion

Changes in forest floor C and N stocks in response to litter input manipulations

Two-year manipulations of aboveground litter inputs substantially changed total amounts of aboveground C and N inputs (Table 1). At the no litter plots, only small

Table 1. Aboveground litter inputs (dry mass, C, and N) during the manipulation period from September 1999 to May 2001 and forest floor C and N stocks measured in May 2001. Forest floor C and N stocks and C/N ratios are presented as means followed by 1SE in parentheses ($n = 3$ for the glucose, 4 for other plots). No litter plots had no distinct Oi material in May 2001. Values followed by different letters are significantly different at $P < 0.05$.

Treatment	Litter input* (g m^{-2})			Forest floor C and N stocks**				
	Dry mass	C	N	C (g m^{-2})		N (g m^{-2})		C/N
				Oi	Oe + Oa	Oi	Oe + Oa	Oi + Oe + Oa
Control	1078	510	12.6	197^{a} (11)	1279 (176)	6.6^{a} (0.4)	72.7 (9.5)	18.6^{a} (0.1)
No litter	137	65	1.6		1165 (194)		62.6 (9.1)	18.4^{a} (0.5)
Double litter	1902	900	22.3	410^{b} (54)	1170 (182)	16.0^{b} (3.2)	63.4 (9.0)	19.9^{b} (0.2)
Glucose	2278	990	12.6	229^{a} (36)	1344 (330)	8.7^{ab} (1.4)	75.7 (16.8)	18.6^{a} (0.2)

*Measured components include foliage, woody debris (twigs and barks) with a diameter <1 cm, and fruit (nuts and acorns) and flower parts.

** Measured for all organic materials except soil macrofauna, undecomposed fruit structures, and woody debris with a diameter >1 cm.

Table 2. Volume-weighted average concentrations of DOC and DON in TF, Oi and Oa leachates, and soil solution (20 cm below the forest floor) over the entire manipulation period from October 1999 to September 2001 and the ratios of DOC/DON. Values are means of three (Oi and Oa leachate data of glucose and all soil solution data) or four (Oi and Oa leachate data of all treatments but glucose and TF) replications ± 1SE. Values followed by different letters indicate a significant difference at $P < 0.05$.

Horizon	Treatment	DOC	DON	DOC/DON
TF		13.1 ± 0.4	0.78 ± 0.03	16.8 ± 1.0
Oi	Control	26.9^{a} ± 2.1	1.02^{a} ± 0.06	26.5^{a} ± 0.6
	No litter	18.2^{a} ± 1.4	1.05^{a} ± 0.06	17.3^{b} ± 0.4
	Double litter	48.4^{b} ± 3.3	1.64^{b} ± 0.09	29.6^{a} ± 1.0
	Glucose	38.6^{b} ± 1.2	1.45^{b} ± 0.04	26.7^{a} ± 1.5
Oa	Control	42.1^{a} ± 5.7	1.44^{a} ± 0.18	29.2^{ab} ± 1.2
	No litter	44.6^{a} ± 7.6	1.94^{a} ± 0.30	23.0^{a} ± 2.7
	Double litter	81.6^{b} ± 12.2	2.52^{b} ± 0.35	32.2^{b} ± 1.7
	Glucose	71.7^{ab} ± 5.0	2.56^{b} ± 0.08	28.0^{ab} ± 1.1
Upper B (20 cm)	Control	16.2^{a} ± 1.3	0.48^{a} ± 0.02	33.4 ± 1.2
	No litter	22.2^{a} ± 1.9	0.66^{a} ± 0.08	33.9 ± 1.4
	Double litter	23.5^{a} ± 3.5	0.72^{a} ± 0.11	32.9 ± 0.8
	Glucose	43.2^{b} ± 3.5	1.23^{b} ± 0.06	35.0 ± 1.1

amounts of litter (approximately 13% of those of the control) reached the forest floor during winter months, in which litter traps were not placed due to snowfall. Doubling of litter inputs from September to December increased the total amount of aboveground litter inputs by 76%, while glucose amendment increased the amount of C input by 94%. The effects of litter manipulations on forest floor C and N stocks were clearly observed in the Oi horizons (Table 1). At the no litter plots, no distinct Oi litter was found in May 2001. At the double litter plots, total amounts of C and N in the Oi horizon were twice those for the control. The four-time applications of glucose (total 480 g C), however, caused no discernable change in C and N stocks either of the Oi or Oe + Oa horizons. The bulk of forest floor C and N stocks was found in the Oe + Oa horizons, which contained 88 and 92% of the forest floor C and N stocks at the control, respectively. No significant change in the C and N stocks of these horizons was observed among treatments. However, the C/N ratios of the whole forest floor significantly increased at the double litter plots (ANOVA, $P < 0.01$), reflecting increased recent litter as a consequence of litter addition.

Responses of DOM concentrations to litter manipulations

For two years following the initiation of manipulations, volume-weighted average concentrations of DOC and DON significantly increased in both Oi and Oa leachates of the double litter and glucose plots compared to those of the control and no litter plots (Table 2). Seasonal variations in DOM concentrations, however, reflected different timing and duration of the response of DOM release to the addition

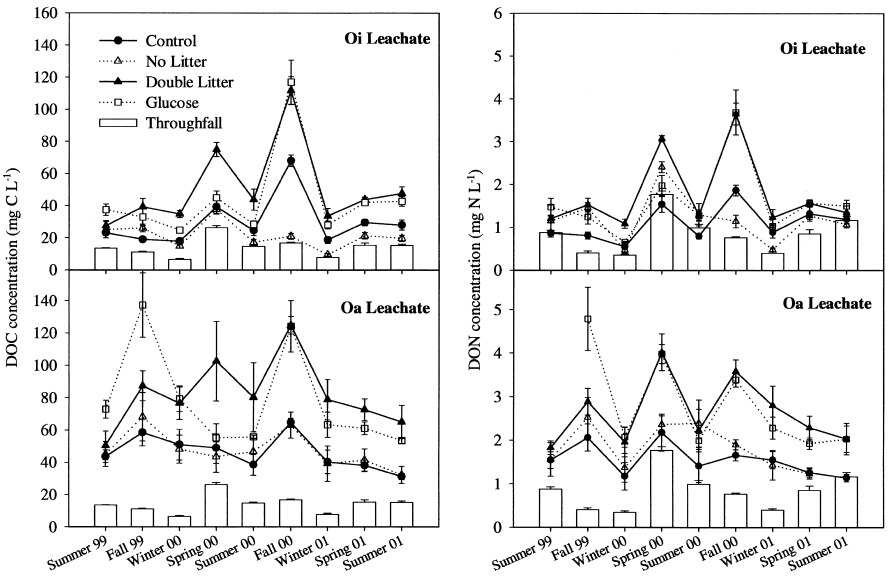

Figure 1. Volume-weighted seasonal average concentrations of DOC (mg C L^{-1}) and DON (mg N L^{-1}) in Oi and Oa leachates and TF. Error bars represent one SE ($n = 3$ for glucose and 4 for other plots and TF concentrations). Note that DOC and DON concentrations in TF are depicted as bars along with both Oi and Oa leachate concentrations. Litter manipulations were initiated in fall 1999 and glucose was applied in fall 1999, summer 2000, fall 2000, and spring 2001.

of two different types of substrates (Figure 1). DOC and DON concentrations in the Oi and Oa leachates of the double litter plots began to increase immediately following the initiation of litter addition and remained constantly higher than those of the other treatments. The application of glucose also caused an immediate increase in both DOC and DON concentrations but the response was generally limited to the glucose applied seasons (fall 1999, summer 2000, fall 2000, and spring 2001).

The calculation of seasonal mean DOC concentrations did not include direct leaching of glucose by excluding leachate concentrations obtained within 4 weeks following the glucose application. Thus, significant increases in DOC concentrations within 2 to 3 months after the glucose application, together with concurrent increases in DON concentrations despite zero N content of glucose, suggest that a temporary growth of microbial population in response to the labile substrate might have increased soluble organic matter through an accelerated decomposition of native organic matter. Considerable increases in DOC and DON concentrations in soil solution from the glucose plots (Table 2) might also reflect a positive effect of increased microbial activity on DOM production in the mineral soil. Soil incubation experiments using ^{14}C-labeled glucose have shown that added glucose is rapidly (within several hours) incorporated into microbial biomass and up to 80% of glucose can be evolved as CO_2 within 2 weeks, accompanying enhanced decomposition of native organic matter (Chahal and Wagner 1965; Haider and Martin 1975; Sugai and Schimel 1993). In a 48 h incubation experiment with a taiga forest

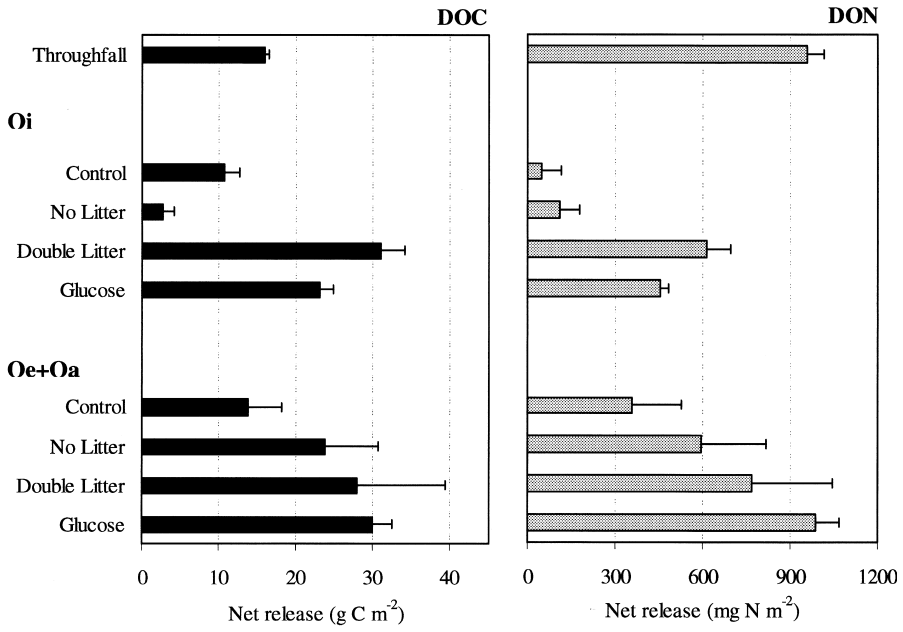

Figure 2. Net releases of DOC and DON from the Oi (fluxes in Oi leachates minus inputs via TF) and Oe + Oa horizons (fluxes in Oa leachates minus fluxes in Oi leachates) over the entire manipulation period from October 1999 to September 2001. Error bars represent one SE ($n = 3$ for glucose and 4 for other plots and TF inputs).

floor, Sugai and Schimel (1993) found that within 4 h, less than 10% of added glucose and phenolics remained unmetabolized (as DOC) in soil solution.

Over the entire manipulation period, no marked changes in DOC and DON concentrations were observed at the no litter plots, with the only exception of decreased DOC concentrations in Oi leachates (Table 2; Figure 1). Litterfall exclusion has reduced DOC concentrations in Oi leachates to the level of TF DOC concentrations since the first summer following the initiation of the manipulation (Figure 1). Although DON concentrations in Oi leachates have also decreased slightly since Fall 2000, it was difficult to find a consistent treatment effect due to small differences in DON concentrations among TF, the control, and no litter plots. The Oa leachates of the no litter plots showed no significant change in the concentrations of DOC and DON throughout the observation period.

Controls over DOM release from different forest floor horizons

To evaluate the contribution of different horizons to forest floor DOM release, net releases of DOC and DON from the Oi horizons (fluxes in Oi leachates minus inputs via TF) and from the Oe + Oa horizons (fluxes in Oa leachates minus fluxes in Oi leachates) were calculated (Figure 2). Almost equal amounts of DOC were

released from each of both horizons at the control, while slightly more DON was leached from the Oe + Oa than the Oi horizons. Net releases of DOC and DON from the Oi horizons were significantly ($P < 0.001$) greater at the double litter and glucose plots than at the control or no litter plots. The net release from the Oe + Oa horizons also tended to be greater at the double litter and glucose plots, but statistically significant differences among treatments were not found due to large within-treatment variations. Despite a slight reduction in DOC release from the Oi horizons, litterfall exclusion increased, on average, net releases of both DOC and DON from the Oe + Oa horizons.

The net DOM release observed for both forest floor horizons at the control, along with the positive response of DOM release at both horizons to litter and glucose additions (Figure 2), suggests an equal importance of different forest floor horizons as a DOM source. In a laboratory leaching experiment with forest floor horizons collected from the study site (Park et al. 2002), each of three horizons was evaluated to make an almost equal contribution to the total release of DOC and DON. The net release of DOC and DON from the lower forest floor horizons conflicts with some past studies (Qualls et al. 1991; Michalzik and Matzner 1999) that observed no further increase in DOC and DON fluxes when the leachate from the upper forest floor (Oi with or without Oe) passes through the underlying horizons. Qualls et al. (1991) performed their study at a deciduous forest floor but included the Oe horizon to the upper forest floor. In their study, therefore, it was impossible to distinguish between the contributions of recent litter and older Oe materials.

Isotopic (^{13}C or ^{14}C) studies on DOM sources in forest soils have recently provided more direct evidence on contributions of various sources ranging from recent litter to humified organic matter to DOM in soil solution and stream waters (Trumbore et al. 1992; Ludwig et al. 2000; Palmer et al. 2001; Hagedorn et al. 2002). Trumbore et al. (1992) found slightly lower or higher ^{14}C contents of DOC in forest floor leachates than those of current leaves (175 $\pm$ 10%), suggesting the contribution of organic matter formed during the last 3 decades or even before 1960 to leachate DOC. In a CO_2-fertilization experiment using open-top chambers, Hagedorn et al. (2002) took advantage of ^{13}C depletion of the added CO_2 to show the low contribution (5–8%) of new carbon source (less than 4-year old) to DOC in soil solution collected at 5–10 cm depth.

To examine the relationship between variations in DOM releases from the Oe + Oa horizons (Figure 2) and changes in microbial activity following litter manipulations, rates of basal respiration and SIR were measured for the Oe + Oa samples collected in May 2001 (Figure 3). Both respiration measurements showed almost equal respiration rates at the control and no litter plots. Rates of basal respiration were slightly greater for the double litter and glucose plots than the control and no litter plots (ANOVA, $P<0.05$). Responses of microbial respiration to glucose addition were also greater at the double litter and glucose plots (ANOVA, $P<0.05$).

Since SIR can be used as a relative measure of metabolically active microbial biomass (Wardle and Parkinson 1990; Ross 1991; Wardle and Ghani 1995), the similar rates of SIR for the Oe + Oa samples from the control and no litter plots suggest that old forest floor horizons can provide resources for the subsistence of

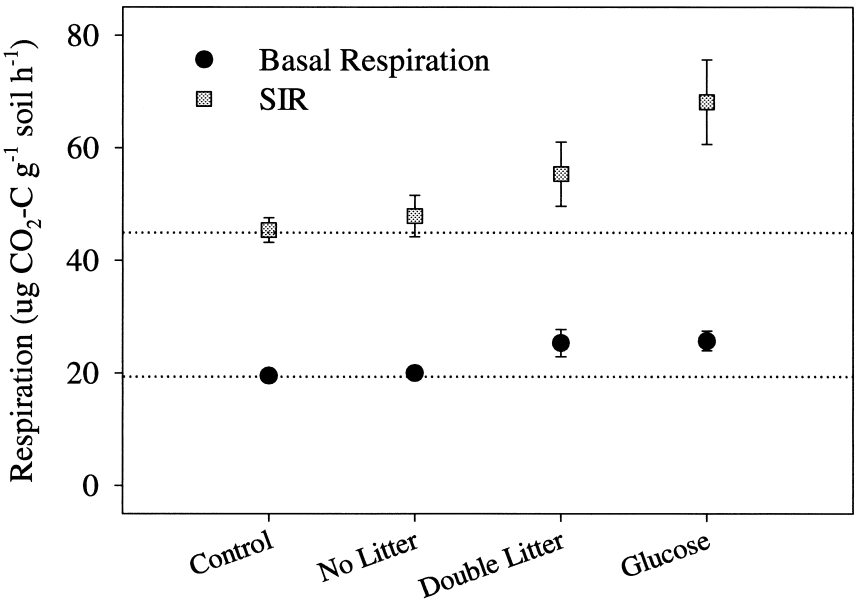

Figure 3. Rates of basal and SIR (μg CO_2-C g^{-1} soil h^{-1}) measured for the Oe + Oa samples collected in May 2001. Error bars indicate one SE ($n = 3$ for glucose and 4 for other plots) and dotted lines the average values of the control.

metabolically active microbes at least for 2 years, despite a substantial reduction in aboveground litter inputs. In a litter removal experiment, Fisk and Fahey (2001) also found no significant reduction in microbial biomass and activity even after 8-year manipulation and ascribed this inconspicuous manipulation effect to the role of belowground C supply in forest floor microbial processes. The efficient utilization of available resources from decomposing old organic materials or TF inputs might also provide possible explanations for the microbial subsistence in the old forest floor horizons without new litter inputs. No significant changes in microbial activity following litterfall exclusion might indicate that the sustained or even slightly increased release of DOC and DON from the Oe + Oa horizons cannot be simply explained by enhanced microbial decomposition of old organic horizon materials. As indicated by lowered C/N ratios of DOM (Table 2), the higher contribution of more humified organic matter to DOM in both Oi and Oa leachates may have reduced microbial consumption of produced DOM in the old forest floor horizons without new aboveground litter inputs.

Over 50% of variations in net releases of DOC from the Oe + Oa horizons over the entire manipulation period were accounted for by differences in initial forest floor depths prior to manipulations (Figure 4). This might indicate that the initial size of organic matter pools has played a crucial role in net DOC releases from the lower forest floor horizons, given that the initial three horizons might constitute the majority of the Oe + Oa horizons over time. By contrast, there was no correlation

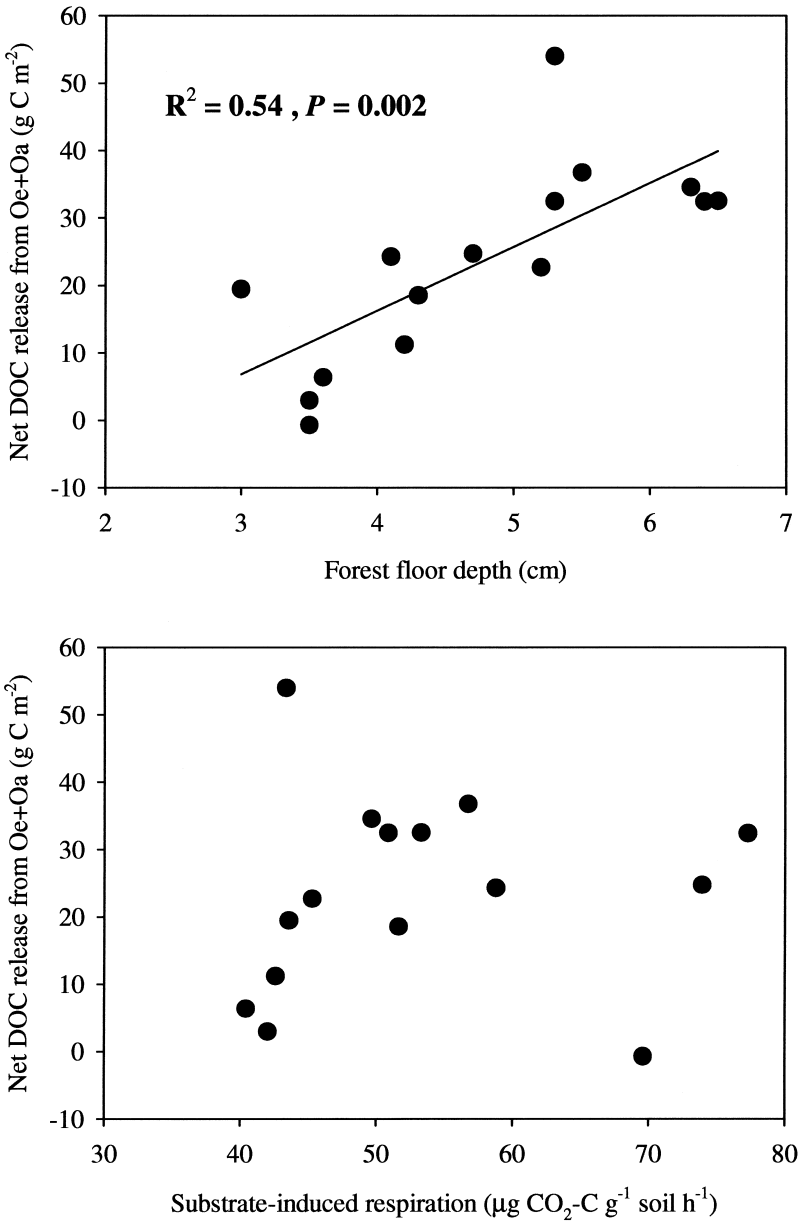

Figure 4. Relationships between net DOC releases from the Oe + Oa horizons over the entire manipulation period (g C m^{-2}) and initial forest floor depths (cm) prior to manipulations or rates of SIR (µg CO_2-C g^{-1} soil h^{-1}) as a measure of microbial activity.

between microbial activity (measured as rates of SIR) in the Oe + Oa horizons and net releases of DOC from these horizons (Figure 4). Since microbial activity was measured at the end of the manipulation experiment, this one-time measurement cannot reflect a series of changes in microbial response to altered resource availability over the 2-year manipulation period. However, these results at least suggest that the actual rates of DOM release from old forest floor horizons cannot directly reflect the complex relationships between resource availability and DOM production and consumption. The sensitive response of DOM release from recent litter pools to altered litter inputs can be explained by the small, labile pools of DOM in the upper forest floor, whereas the release patterns in old forest floor horizons seem to depend on the initial size of source pools. It is still unclear whether increased DOM inputs from the Oi horizon following litter additions simply pass through the underlying horizons without chemical alteration. Considering that the composition of DOM released from recent litter constantly changes during the passage through the soil horizons (Kaiser et al. 2002), microbial transformation of labile DOM components should not be ruled out, as indicated by changing C/N ratios of DOM during the movement through the organic horizons and mineral soil (Table 2).

DOM as a vehicle for C and N export from the forest floor

To evaluate the significance of DOM leaching for C and N losses from the forest floor, annual fluxes of DOC and DON were compared to other C and N pools and fluxes (Figure 5). DOM released from the forest floor accounted for approximately 8 and 11% of annual litterfall C and N inputs at the control, respectively. Leaching loss of C is estimated to amount to 13% of annual total C loss (respired C plus leached C) from the forest floor, using an estimation of annual heterotrophic respiration based on the measured respiration rate of forest floor samples collected at the study site in a 98-day incubation experiment (Park et al. 2002). Because our respiration estimate may overestimate the actual forest floor respiration given the incubation of disturbed samples under optimal laboratory conditions, the contribution of DOC loss to the total forest floor C loss can be much higher than 13%.

Past studies have shown that DOC release from deciduous forest floors ranges from 3 to 18% of annual litterfall C (McDowell and Likens 1988; Qualls et al. 1991; Hongve et al. 2000). In some field and laboratory experiments, DOC release was estimated to represent 8 to 35% of total C loss from the forest floor (Yavitt and Fahey 1986; Vance and David 1991; Wagai and Sollins 2002). Annual C and N losses via leaching, along with the pools of readily soluble organic matter and microbial C, were relatively small compared to total C and N stocks of the forest floor. Pools of microbial C (30.6 g C m^{-2} in the whole forest floor) were larger than annual DOC loss as well as pools of K_2SO_4-extractable organic C (as a measure of soluble organic C), suggesting rapid microbial turnover of available C sources, either in TF or from decomposing forest floor materials, prior to leaching loss.

Despite the relatively small flux compared to C mineralization, DOC in forest floor leachate represents one of the primary C inputs to the mineral soil, along with

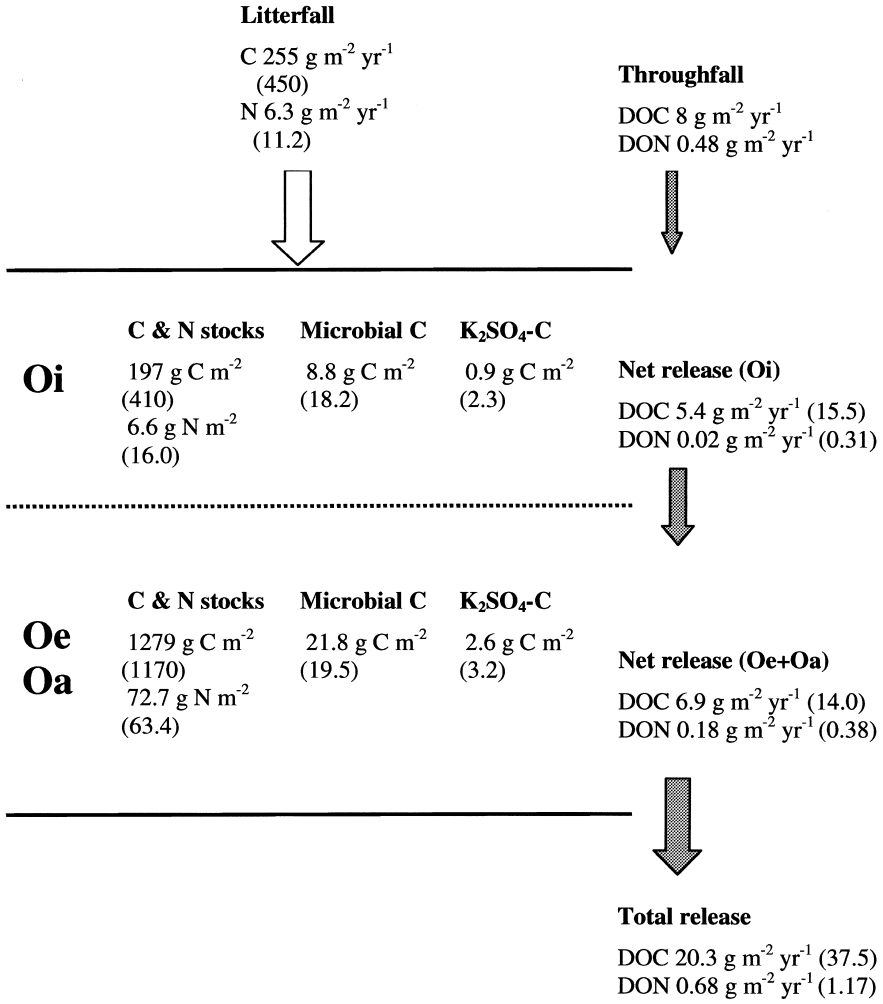

Figure 5. Pools (g C m^{-2}) and fluxes (g C m^{-2} $year^{-1}$) of C and N in the forest floor of the control and their responses to litter addition (in parentheses). C and N pools were measured in May 2001 and the annual fluxes of DOC and DON are means of two-year fluxes. K_2SO_4-C represents soluble organic C extracted with 0.5 M K_2SO_4 solution.

root exudates and detritus (Zech et al. 1996; Richter et al. 1999). Little is known as to how altered DOC fluxes by changes in forest management (e.g., clear-cutting or reforestation) or environmental conditions (e.g., warming or rising atmospheric CO_2) will impact C dynamics in the underlying mineral soil. Recent free-air CO_2 enrichment experiments have shown that enhanced tree growth under elevated atmospheric CO_2 concentrations can lead to an increase in litterfall and DOC fluxes via TF (DeLucia et al. 1999; Lichter et al. 2000). In this study, the addition of aboveground litter inputs increased DOC release from the forest floor by 83%,

suggesting a sensitive response of forest floor DOM dynamics to an increase (76%) in aboveground litter inputs (Figure 5).

Despite almost doubled DOM release from the forest floor under increased litter inputs, DOC and DON concentrations in soil solution collected at 20 cm depth below the forest floor showed no clear difference from those of the control, suggesting a strong buffering effect of the mineral soil horizons on DOM fluxes (Table 2). Some CO_2 enrichment studies also reported that DOC concentrations in soil solution were not responsive to litter input increases via enhanced root turnover (King et al. 2001; Hagedorn et al. 2002). Although drastic reductions in DOM fluxes in the mineral soil are generally associated with strong sorption capacity of the mineral soil (Qualls and Haines 1992; Kaiser et al. 1996), the possibility of increased biodegradation of labile DOM compounds under elevated C inputs has also been suggested (Hagedorn et al. 2002).

Significance of water flux in mobilizing DOM: results of TF manipulation

By manipulating TF fluxes, we expected that concentration changes following manipulation would reveal the magnitude of additional DOM sources in the forest floor. Both DOC and DON concentrations decreased significantly in Oi leachates relative to those of the control, while no reduction in concentration was found for Oa leachates (data not shown). Net releases of DOC from each of the two forest floor horizons showed that additional amounts of DOC released by doubled TF fluxes were primarily derived from the Oe + Oa horizons (Figure 6). In contrast to slight reductions in the net release from the Oi horizon since the second season following the initiation of the manipulation, the Oe + Oa horizons released substantial amounts of additional DOC in response to increased water fluxes throughout the manipulation period. DOM released from the forest floor by percolating water may be derived not only from soluble organic matter in fresh litter but also from some parts of solid organic matter that can be solubilized under favorable conditions (Tipping 1998). The presence of the pools of this 'potential DOM' in the forest floor was confirmed by correlations between the frequency or intensity of hydrologic flushing and the amount of DOM released (Christ and David 1996a; Gödde et al. 1996; Judd and Kling 2002). Considerable increases in net DOC release from the Oe + Oa horizons in response to increased water fluxes suggest that the majority of potential DOM exists in the lower forest floor horizons at this site.

Some field data showed that the fluxes of DOC and DON in forest floor leachate increased with increasing water fluxes (Michalzik et al. 2001; Solinger et al. 2001), in contrast to the results showing a dilution effect of increasing water fluxes on DOC concentration (McDowell and Wood 1984; Easthouse et al. 1992). In a field manipulation study, Tipping et al. (1999) found that increased water fluxes can enhance DOC export only from some soil types with relatively large pools of potential DOM. Qualls (2000) contended that these pools of potential DOM exist in fresh litter and DOM release from these pools decreases gradually due to a sorption

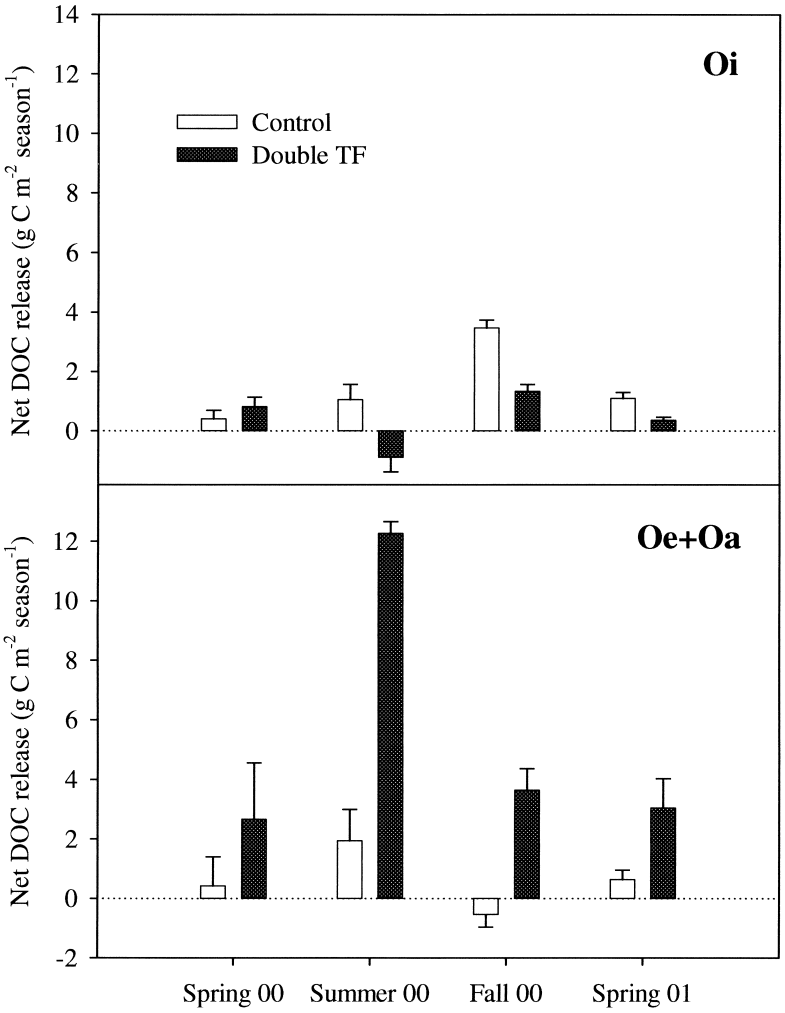

Figure 6. Net releases of DOC from the Oi (fluxes in Oi leachates minus inputs via TF) and Oe + Oa horizons (fluxes in Oa leachates minus fluxes in Oi leachates) during the seasons in which TF doubling was performed. Error bars indicate one SE ($n = 4$).

constraint in the forest floor. Our results showed that the size of potential DOM pools in the upper forest floor (including fresh litter) is relatively small compared to that of the lower horizons. The large pools of potentially soluble organic matter in the lower forest floor horizons are consistent with the finding of the pool size control on net DOC release from the Oe + Oa horizons (Figure 4). Despite uncertainties regarding the exact origin and mobilization processes, the increased DOM release from the pools of potential DOM suggests that water flux can play a key role in mobilizing DOM from the forest floor unless the magnitude of the pools is small.

Conclusions

DOM release from the forest floor represented approximately 10% of annual aboveground litter C and N inputs at the control. Comparison of DOM release patterns among forest floor horizons and treatments suggested that DOM in forest floor leachate is derived not only from recent litter but also from older organic matter in the lower forest floor horizons. Although some recent biogeochemical models included DOM fluxes through soils as an important component of internal ecosystem C and N cycling, these models generally assume that humus in lower forest floor horizons does not contribute to the DOM leaching losses from the forest floor (Currie and Aber 1997; Neff and Asner 2001). We propose that DOM release from the forest floor should represent the leaching from older organic matter pools as well as recent litter. Further research will be needed to elucidate different chemical characteristics of DOM released from various DOM sources in different forest floor horizons and their effects on bioavailability and sorption behavior of the released DOM in the mineral soil.

Our results indicated a sensitive response of DOM release mechanisms in recent litter pools to changed litter inputs and a complex interaction between the production and retention of DOM in the lower forest floor horizons and mineral soil. Although increases in microbial activity were detected for the Oe + Oa horizons in response to the addition of litter and glucose, the enhanced microbial activity was not simply translated into an increase in net DOM release from these old organic horizons. Since DOM release from the forest floor is a net result of microbial production and consumption and hydrologic transport, actual amounts of DOM in forest floor leachates may not necessarily reflect changed production rates in response to altered resource availability. Thus, the magnitude of potentially soluble organic matter and water flux seems to play a more important role in regulating the actual DOM release from the forest floor than a straightforward relationship between microbial activity and DOM production.

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