



Dissolved organic carbon production and flux under long-term litter manipulations in a Pacific Northwest old-growth forest

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Abstract Dissolved organic carbon (DOC) flux is an important mechanism to convey soil carbon (C) from aboveground organic debris (litter) to deeper soil horizons and can influence the formation of stable soil organic C compounds. The magnitude of this flux depends on both infiltration and DOC production rates which are functions of the climatic, soil, topographic and ecological characteristics of a region. Aboveground litter quantity and quality was manipulated for 20 years in an old-growth Douglas fir forest under six treatments to study relationships among litter inputs, DOC production and flux, and soil C dynamics. DOC concentrations were measured at two depths using tension lysimeters, and a hydrologic model was created to quantify water and DOC flux through the soil profile. DOC concentrations ranged from 3.0–8.0 and 1.5–2.5 mg C/L among treatments at 30 and 100 cm below the soil surface, respectively. Aboveground detrital inputs did not have a consistent positive effect on soil solution DOC; the addition of

coarse woody debris increased soil solution DOC by 58% 30 cm belowground, while doubling the mass of aboveground leaf litter decreased DOC concentrations by 30%. We suggest that high-quality leaf litter accelerated microbial processing, resulting in a “priming” effect that led to the lower concentrations. Annual DOC flux into groundwater was small (2.7–3.7 g C/m²/year) and accounts for < 0.1% of estimated litter C at the site. Therefore, direct DOC loss from surface litter to groundwater is relatively negligible to the soil C budget. However, DOC flux into the soil surface was much greater (73–210 g C/m²/year), equivalent to 1.4–2.4% of aboveground litter C. Therefore, DOC transport is an important source of C to shallow soil horizons.

Keywords DIRT · Dissolved organic carbon · DOC · H.J. Andrews Forest · LTER

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Introduction

Soil organic matter (SOM) is the largest terrestrial carbon (C) sink in the biosphere and can change in relatively short geologic time scales (Pan et al. 2011; Schlesinger 1997). Approximately 45% of global forest C is stored in the top meter of soil (Pan et al. 2011), whereas the remainder is distributed in aboveground organic debris (litter), deadwood, and live

biomass. Because the global SOM pool is so large, a small percent change in storage can have profound impacts on the atmospheric C pool. Schimel et al. (2000) found that C flux in the U.S. from soil to the atmosphere via decomposition of organic matter and root respiration was approximately 10-fold greater than fossil fuel and deforestation sources combined. Net primary production in northern temperate ecosystems is generally predicted to increase in the future from changing climatic conditions (Melillo et al. 1993), which will increase carbon inputs to the soil. However, the link between litter quantity and soil C stabilization are not direct and may be ecosystem dependent (Fröberg et al. 2006; Crow et al. 2009a, b). Therefore, it is critical to understand how the SOC pool will respond to these litter changes so future predictions of global C storage are accurate.

Dissolved organic carbon (DOC) from litter decomposition can convey C from aboveground litter to deeper soil horizons and has the potential to be an important flow in the soil C budget. The magnitude of this flux relies on both infiltration and DOC production rates which are functions of the climatic, soil, topographical and ecological characteristics of a region. Past studies have established that relatively little DOC produced in organic horizons gets transported to groundwater (Yano et al. 2005; Lajtha et al. 2005; Creed et al. 2008). Transport of DOC from surface litter through the soil profile is inhibited by sorption between DOC and the soil matrix, and by direct assimilation and mineralization by soil microorganisms. The DOC that does reach groundwater, links terrestrial and aquatic ecosystems through the transport of C from soils to streams (Fellman et al. 2009). Creed et al. (2008) estimated that annual DOC flux from 33 forested catchments varied from 0.9 to 13.9 g C/m²/year. Similarly, Lajtha et al. (2005) estimated a flux of 2.0–3.8 g C/m²/year for different aboveground litter types. These estimates revealed that a small mass of C is lost from the soil system through this pathway. However, a significant quantity of C from aboveground litter can be transported into shallow soil horizons as DOC under high leaching rates (Lee et al. 2018; Cleveland et al. 2004). O-horizon DOC concentrations under forest floor litters have been reported to range from 30 to 120 mg C/L which is an order of magnitude higher than soil solution concentrations (Solinger et al. 2001; Lajtha et al. 2005; Fröberg et al. 2006). These surface concentrations can result in

larger C fluxes into the mineral topsoil relative to the reported DOC fluxes into groundwater. For example, Solinger et al. (2001) reported a DOC flux of 20–35 g C/m²/year which is an order of magnitude greater than DOC flux into groundwater estimated by Lajtha et al. (2005).

Soil DOC concentrations can impact microbial respiration rates and the formation of stabilized mineral associated organic matter (MAOM; Córdova et al. 2018; Cotrufo et al. 2013). Cotrufo et al. (2013) proposed the microbial efficiency matrix stabilization theory (MEMS) which states that microbial substrate use efficiency controls the relative proportion of C which is lost through respiration versus C that is stored as stable SOM. MEMS suggests that labile plant constituents are the primary precursors to stable SOM because they are utilized most efficiently by microbes, and microbial products synthesized from C assimilation then dominate the stable SOM pool. This hypothesis has been supported by both field and incubation studies (Bradford et al. 2013; Cleveland et al. 2004). Yet, other studies have shown that high quality labile litter may induce microbial priming of SOM (Crow et al. 2009a, b; Córdova et al. 2018; Sulzman et al. 2005). Priming is a widely observed microbial phenomena where the addition of a labile substrate increases the mineralization of a more stable substrate. Córdova et al. (2018) found that higher respiration rates, associated with C utilization from labile litter sources, caused a net decrease in the conversion of litter C to MAOM. These discrepancies reveal that there is not yet a clear consensus on the role of litter quality in stable SOM formation. However, it is apparent that DOC must play a key role in the formation of soil C stocks since the conversion of litter C to DOC, and then DOC utilization by microbes, is a limiting factor for SOM accumulation. It is important to unravel this relationship so that forest practitioners may implement future management practices that increase formation rates of stable SOC, and therefore improve the soils ability to function as an atmospheric C sink.

The objectives of our study were 2-fold: (1) to determine the importance of DOC flux in the soil C budget relative to aboveground litter supplies, and (2) to determine how litter quality and quantity influence DOC production rates and microbial utilization of this DOC. To achieve our objectives, we performed litter manipulations that excluded aboveground litter and

roots, or supplemented natural detrital inputs with woody debris or leaf/needle litter. In the litter exclusion plots, soil C pools have been depleted (Lajtha et al. 2018), thus we hypothesized that DOC would decline over the course of the study period. Microbial processing of the added litter in the double litter (DL) and double wood (DW) treatments was expected to increase DOC production rates. Further, we hypothesized that priming-induced consumption of DOC in the DL treatment could outweigh the effect of increased inputs from aboveground litter which would cause a net decrease in DOC concentrations. Priming would occur in this case because DOC derived from leaf litter has a high proportion of labile substrate relative to the other treatments (Yano et al. 2005) which could increase the mineralization of DOC that was formerly stable. The DOC derived from the DW litter is generally more recalcitrant, so we hypothesized that the DW treatment would have the highest DOC concentration among all litter treatments. We expected these differences to be most significant in surficial soils, yet we anticipated that retention of DOC in the soil profile would effectively homogenize concentrations between treatments 100 cm below the surface.

Methods

Study site

This study was conducted at the H.J. Andrews Experimental Forest located in Oregon's Western Cascades. The experimental forest was founded in 1948 by the US Forest Service and it is now a hub for long term ecological research (LTER). H.J. Andrews is part of the National Science Foundation funded LTER Network and offers an extensive database of meteorological and ecological observations from its inception to the present. Mean annual precipitation is 2080 mm/year and mean temperature at the forest headquarters is 9.4 °C (averaged from 1999 to 2014). Over 70% of annual precipitation occurs during a "wet period" between November and March (Sollins et al. 1980).

The study site for the detrital input and removal treatment (DIRT) experiment was established in an undisturbed old growth Douglas fir (*Pseudotsuga menziesii*) and Western Hemlock (*Tsuga*

heterophylla) forest at an elevation of approximately 720 m. The study site also contains Western Red Cedar (*Thuja plicata*), Vine Maple (*Acer circinatum*), Big-Leaf Maple (*Acer macrophyllum*), Red Huckleberry (*Vaccinium parvifolium*) and Oregon Grape (*Mahonia aquifolium*). The soil surface is covered with mosses and a diverse community of ground cover species. The soil is derived from volcanic parent material and classified as coarse loamy mixed mesic Typic Hapludands. Small areas of Andic Dystrudepts and Vitrandic Dystrudepts also underlie the treatment plots (Yano et al. 2005; Spears and Lajtha 2004; Lajtha et al. 2005).

Six litter treatments were established at the DIRT plots in 1997. These treatments include the addition of coarse woody debris and leaf litter, and the exclusion of litter and roots by screening and trenching (Table 1). Each treatment was replicated 3 times ($n = 3$) and assigned random plot locations. The plots are 10 × 15 m and include trees and other natural features. Trees and all other live vegetation were removed from the no input (NI) and no root (NR) treatments during site creation. Litter was excluded from the NL and NI treatments using 1 mm mesh screening to collect all falling debris. All litter material was initially removed and kept bare on these plots. Litterfall from the NL plots has been systematically collected and transferred to the DL plots. In early stages of the study, litter was collected 4–5 times per year: at the end of the dry season, twice or more during the wet season (November to March), and at the beginning of the dry season (Lajtha et al. 2005). In the past 10 years litter has been collected and transferred on an annual basis during the dry season. This method of removal does allow some DOC flux into the NL and NI plots because the organic debris is not immediately removed from the screens.

A mix of decomposed woody debris and shredded chips (5–20 cm in length) of Douglas-fir wood with a ratio of decomposed woody debris to intact woody debris of 4:1 have been added every other year to the double wood treatment plots (Lajtha et al. 2005). The mass of this addition was estimated to be equal to falling wood debris in the control plots. Logs were obtained from a local mill and were chipped by Rexius of Eugene, Oregon. Roots were excluded from the NR and NI treatments using an impermeable barrier at the plot boundaries as deep as the C-horizon (Lajtha et al. 2005).

Table 1 DIRT plot treatments at H.J. Andrews LTER site

Treatment	Method
Control (CTL)	Normal litter inputs
Double litter (DL)	Aboveground needle/leaf litter is doubled by adding litter removed from NL plots
Double wood (DW)	Aboveground wood inputs are doubled by adding large shredded wood debris based on measured input rates of woody debris fall
No litter (NL)	Aboveground litter inputs are excluded from plot
No roots (NR)	Roots are excluded with impenetrable barriers extending from the soil surface to the top of the C horizon
No inputs (NI)	Aboveground inputs are prevented as in NL plots; belowground inputs are prevented as in NR plots

Lysimeter water collection and analysis

Five Prenart Superquartz tension lysimeters were installed at a 30° angle in each treatment plot in 1997 to extract water samples from the soil matrix. Two of the lysimeters were installed to a depth of 100 cm and three were installed at 30 cm in each plot according to the method described by Lajtha et al. (1999). The lysimeters were sampled on a monthly basis during the first three years of the DIRT study and were subsequently sampled multiple times per year until 2008. The consistency of sampling events decreased as the study progressed and no samples were obtained in 2009–2013. Lysimeter sampling resumed from 2014 to 2017 but was limited to two sampling events in 2014 and a single sampling event in the years 2015–2017. Not all lysimeters or plots were sampled during every sampling event because soil water content was too low for sampling or the lysimeter was not able to maintain a negative suction force. Samples were only collected during the wet season (October to May) when sufficient soil moisture was available for water extraction. All samples were collected within 72 h of tension (− 50 kPa) being applied to the lysimeters. After extraction, samples were stored on ice and transferred to Oregon State University where they were frozen until analysis. Water samples were analyzed for DOC through Pt-catalyzed high-temperature combustion using a Shimadzu TOC analyzer.

A single zero tension lysimeter was installed at the bottom of the O-horizon in DW, DL, and CTL plots in 2000 (Lajtha et al. 2005). These lysimeters were installed by placing a 20 cm × 20 cm plastic container at the soil surface after carefully removing an

identically sized O-horizon quadrant. This O-horizon material was then placed back directly on top of the lysimeter. O-horizon leachate was collected from these lysimeters during the wet season of 2000–2001 and analyzed for dissolved organic DOC as described by Lajtha et al. (2005). The zero tension lysimeters were removed from the plots after the 1-year sampling effort. The results from this study were used to extrapolate DOC concentrations between the soil surface and the 30 cm lysimeters.

Field methods

Saturated hydraulic conductivity of the soil surface was measured at the study site using a single ring permeator. Measurements were taken at randomly chosen plot locations where the mineral soil surface could be easily accessed. Natural obstacles including fallen logs, decaying wood or root channels were avoided to ensure consistent measurements. Avoiding all uncharacteristic regions was not possible, so outliers greater than 1.5 × the interquartile range, were removed from the dataset. Each plot was sampled at nine locations (n = 9) resulting in a total of 27 observations per treatment. The Ks was calculated from field data using Darcy's law, the Green and Ampt model assumptions (Green and Ampt 1911), and an estimated soil water content and porosity.

Litter mass was measured in each treatment using a 150 cm² quadrant from each plot (n = 3). The organic material collected from this quadrant was dried in an oven at 60 °C for 24 h and then weighed. This mass was converted to total litter C utilizing previous data reported by Yano et al. (2005) for litter C content by treatment. The calculated aboveground litter C stocks,

and the estimated DOC flux, were used to determine the relative mass of C lost from litter through DOC flux annually.

Hydrus model

A computational simulation was completed using an open-source numerical modeling software (PC-Progress HYDRUS-1D) to estimate the cumulative and annual water flux out of each treatment at multiple soil depths. This software was created for the analysis of water flow and solute transport in variably saturated porous media (Simunek et al. 2013). The simulated water flux and measured DOC concentrations were used to approximate annual DOC flux. The software uses a one-dimensional finite element model that solves the Richards–Richardson flow equation to simulate the movement of water, heat and solutes. The major processes we included in the simulation were: water flow in a heterogenous soil profile, root water uptake, and evapotranspiration calculated using the Penman–Monteith equation. Daily meteorological data were accessed from the HJ Andrews Experimental Forest PRIMET Station from 1 January 1999 to 31 December 2014 and included daily precipitation, solar radiation, wind speed, relative humidity and air temperature. The PRIMET Station is located approximately 4 km from the DIRT site. The H.J. Andrews Experimental Forest Database is publicly available under a creative commons license (<https://andrewsforest.oregonstate.edu>, Daly 2019). Boundary conditions were defined at the mineral soil surface, and 150 cm belowground. The upper boundary condition was specified as an “Atmospheric Boundary Condition with Surface Runoff” and the lower boundary condition used was “Free Drainage”. An atmospheric boundary condition requires user-provided meteorological data to compute water flux into the soil profile, if precipitation exceeds the soil’s ability to infiltrate water then that precipitation turns into surface runoff. The free drainage boundary condition imposes a zero-pressure head gradient at the bottom of the soil profile, which is appropriate to implement when the water table is relatively far away from the lower boundary. This assumption was valid because the study site is located at a high elevation hillslope far from the closest stream and we did not have groundwater data immediately available to us.

The simulated soil profile was split into three horizons at 0–20 cm (A-horizon), 20–70 cm (B-horizon) and 70–150 cm (C-horizon). Each horizon had a specified tortuosity, porosity and residual water content which were calculated from soil texture, and a specific Ks which was informed by direct surface measurements. The Van-Genuchten model was used to simulate soil water flux using these hydraulic properties. Root water uptake was estimated using the Feddes model with input parameters from a default dataset for deciduous fruit trees (Feddes et al. 1978). This was the best alternative to coniferous tree data which were unavailable in the literature. Roots were included in the soil profile from 0 to 100 cm, which is usually the lower extent for Douglas fir trees (McMinn 1963). The root density was set to decrease dramatically with soil depth, with approximately 50% of total root mass in the top 20 cm of soil.

After the core model was created in Hydrus, the simulation was computed from 1 January 1999 to 31 December 2014 (5844 days) for each DIRT treatment using an initial water content at field capacity. The maximum specified time-step was 0.01 days. Each DIRT treatment received the same input data and hydraulic properties except for measured differences in Ks. Transpiration and root water uptake were excluded from the NI and NR plots.

Model results were validated systematically using HJ Andrews meteorological data, input soil properties, Darcy’s law calculations, and a sensitivity analysis. We completed a water mass balance on all model fluxes and confirmed that annual precipitation was equivalent to the sum of all water losses including root water uptake, evaporation, runoff and infiltration. We ensured that predicted soil moistures ranged between the specified residual and saturated moisture content and followed expected seasonal trends. To validate root water uptake and evaporative water losses, we calculated the maximum daily evaporation at the project site using the maximum daily solar radiation from our input dataset. We found that our calculated 1.2 cm/day closely matched the maximum daily root water uptake predicted by the model. Further calculations were completed on randomly chosen days in the simulation to validate water flux estimates through the soil profile. We used the model output moisture content, the effective hydraulic conductivity of the soil profile, a Van-Genuchten soil water characteristic curve, and daily precipitation rates to estimate water

flux at different soil depths using Darcy's law. These calculations were compared to simulated daily water flux estimates.

A sensitivity analysis was completed on four parameters including (1) the "free drainage" lower boundary condition, (2) effective K_s , (3) Feddes root water uptake wilting point pressure and (4) leaf area index. These variables were perturbed by $\pm 25\%$ and the model was computed with the new input value. Absolute change (%), relative sensitivity, and absolute sensitivity were tabulated for annual average flux at 10 and 100 cm. The perturbed input variables had little impact on the predicted annual average water flux at 10 and 100 cm suggesting that the simulation was primarily driven by the input daily meteorological data that controlled precipitation and root water uptake rates.

DOC flux calculations

The average DOC concentrations at 30 cm and 100 cm were multiplied by the Hydrus predicted water flux for each treatment to obtain a DOC mass flux. Surface DOC flux was also estimated in this way. DOC surface concentration data were available from measurements completed by Lajtha et al. (2005) that utilized zero-tension lysimeters placed immediately under the O-horizon. The data were only available for the DW, DL and CTL treatments, as removal treatments do not have O horizons. The DOC flux 10 cm belowground was determined from a linearly interpolated concentration.

Data analysis and statistics

Before analysis, the DOC concentration data from the respective soil depths of 30 cm and 100 cm were averaged by plot, providing a total of three replicates per depth and treatment type for each sampling date. Seasonal trends in DOC concentration for each treatment and depth were assessed using data from the first 10 years of the study (1997–2006), when sampling dates and the number of samples recovered from each plot were most frequent. We tested for seasonal effects using both monthly and seasonally averaged DOC concentrations from each plot. For the seasonal averages, Fall included months October to December, Winter included months January to March, and Spring included months April to May. Summer

was not included since no samples were collected in the dry season from June to September. Seasonal differences in DOC concentrations were determined using a linear mixed effects model with either month or season as the fixed effect. Plot and treatment type were included in the model as random effects to account for treatment effects and repeated measures from the same plots over time.

Litter treatment effects on DOC concentrations were analyzed over the full, 20-year study period using mean plot DOC concentrations from 30 and 100 cm. Initially, we tested for treatment effects on DOC concentrations over time at both depth increments using a linear mixed effects model with year, treatment and the interaction between year and treatment included as fixed effects. Plot was also included in the model as a random effect to account for repeated measures. Based on an analysis of variance (ANOVA), time was not found to have a significant effect on DOC in this model, indicating the magnitude of treatment effects did not significantly change over the study period. Thus, we revised our statistical analysis to test for treatment effects on DOC concentrations irrespective of study time by adjusting our linear mixed effects model to include treatment as the only fixed effect, while retaining plot as a random effect. Post hoc Tukey honest significant difference (HSD) tests were then performed to ascertain significant differences among pairwise combinations of treatments.

A linear model was used to compare mean saturated hydraulic conductivity (K_s) measurements between treatments. Analogous to the DOC concentrations, an ANOVA was used to determine if treatments effects were significant and post hoc Tukey HSD tests were then performed to find specific significant differences among pairwise combinations of treatments. Time was not included in this analysis since hydraulic conductivity was only measured at the end of the study. Statistical differences were defined as significant at $\alpha = 0.05$. Statistical analyses were performed using R version 3.5.2 (R Core Team 2019) and the lme4 package (Bates et al. 2014).

Results

There were no differences in water flux between treatments at the soil surface, yet a higher flux was

observed at 30 and 100 cm in the soil profile for the NI and NR treatments because these treatments had no water loss to root water uptake (Table 2). The annual average water flux from the control Hydrus model was 208, 156 and 150 cm/m²/year at 0, 30, and 100 cm respectively. The model output revealed that the soil profile remained unsaturated during the entire 16-year simulation because soil infiltration rates were much greater than the maximum input precipitation rate. Ks field measurements revealed significant differences in infiltration rates among treatments ($p < 0.001$, Fig. 1). Despite the different Ks values for each treatment, annual water flux at all depths were similar for treatments that included roots because all precipitation infiltrated through the soil matrix. The DW treatment had the highest Ks, approximately 300 cm/day greater than the CTL treatment ($p = 0.031$). The Ks of the NI manipulation was approximately 100 cm/day less than the CTL treatment, but this was not significant ($p = 0.39$). The NL treatment was not significantly different than the CTL or the NI manipulation ($p = 0.79, 0.96$ respectively).

The litter manipulation treatments led to significant effects on DOC concentrations at 30 cm soil depth over the entirety of the 20-year study period ($p < 0.001$, Fig. 2; Table 3). DOC concentrations ranged from 3.0–8.0 and 1.5–2.5 mg C/L among treatments at 30 cm and 100 cm below the soil surface, respectively (Table 3). Treatment effects on DOC concentrations occurred rapidly and were consistent throughout the study, as we found no significant temporal trends in DOC concentration across monthly, seasonal and annual timescales. While not significant ($p < 0.20$), the NR treatment was the only litter manipulation treatment to show any evident sign of a long-term linear effect on DOC concentration. However, the NI treatment, where surface litter inputs were

Table 2 Annual average water flux predicted by Hydrus simulation at three depths reported in cm/year

Annual average water flux (cm)						
Depth (cm)	CTL	DW	DL	NL	NI	NR
0	208	208	208	208	207	207
30	156	156	156	156	207	207
100	130	130	130	130	205	205

Flux was predicted for all treatments

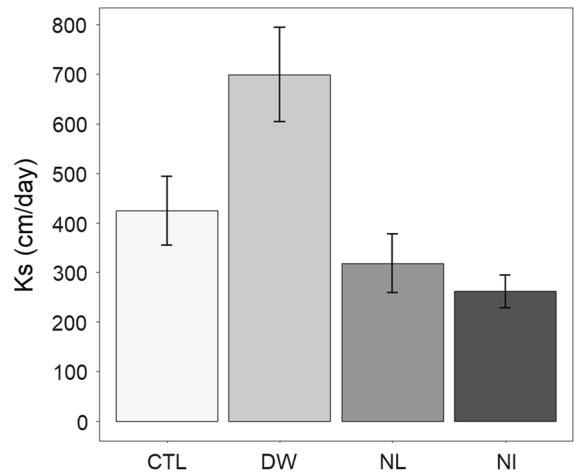


Fig. 1 Average saturated hydraulic conductivity (Ks) (\pm SE) from single ring permeator measurements reported in cm/day. Treatment groups were statistically different ($p < 0.001$)

removed along with the cessation of root activity, did not show similar signs of a linear increase in DOC over time.

Increases in aboveground detrital inputs did not have a consistent effect on soil solution DOC 30 cm belowground. Additions of coarse woody debris increased the 30 cm DOC concentration by 2.5 ppm (+ 58%, $p < 0.001$), while doubling the input of aboveground leaf litter decreased 30 cm DOC concentrations by 1.0 ppm (– 30%, $p < 0.001$). The litter exclusion treatments had the lowest DOC concentrations, which were all approximately 2.5 ppm lower than the CTL treatment ($p < 0.001$ for all three treatments), and were not substantially different from each other ($p > 0.10$). Mean DOC concentrations at 100 cm were not statistically different among treatments ($p = 0.23$) and no group was significantly different from the CTL (Fig. 2).

The estimated water flux (Table 2) and DOC concentration data (Table 3) were used to quantify DOC mass flux from each treatment (Table 4). DOC flux into the soil surface ranged between 73 and 210 g C/m²/year for the CTL, DW and DL treatments. This flux decreased drastically as water progressed through the mineral horizons, with a range of 2.7–3.7 g C/m²/year. At 100 cm belowground, the DOC flux was considered to be the DOC entering groundwater (i.e., no more DOC was lost to sorption or microbial uptake). The DW treatment experienced a DOC mass flux nearly three times higher than the CTL treatment

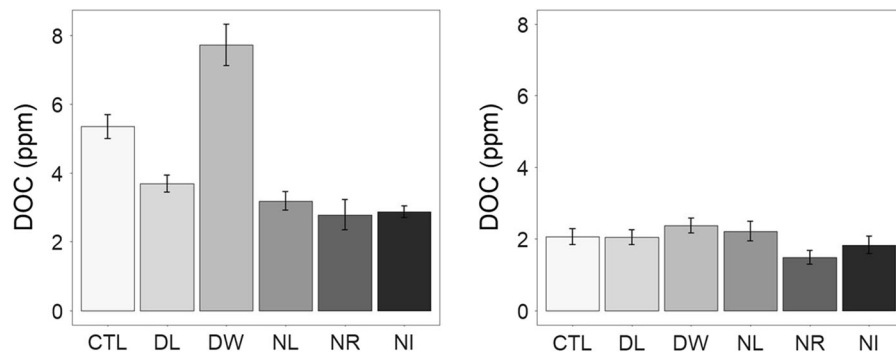


Fig. 2 Average DOC concentration 30 cm belowground (left) and 100 cm belowground (right) by treatment for all sampling events. Groups were statistically different from the linear fixed

effects model ($p < 0.001$) 30 cm belowground. Groups were not statistically different at 100 cm

at the surface and in shallow soil horizons (Table 4). This flux was effectively homogenized deeper in the soil profile and stabilized near the same value as the CTL at 100 cm. The DL treatment had an estimated surface flux that was $\sim 40\%$ higher than the CTL treatment, but this flux decreased more rapidly with depth than the CTL treatment and was 45% lower than the CTL 30 cm belowground. Litter exclusion treatments (NL/NR/NI) experienced the smallest DOC mass flux which was approximately 75% less than the CTL 30 cm belowground (Table 4). However, the flux at 100 cm was greater for these treatments than the CTL and DL plots. The NI and NR treatments had the highest DOC flux out of any treatment at 100 cm because the exclusion of root water uptake caused a greater annual water flux.

Discussion

Seasonal trends

Seasonal DOC trends have not been detected in soil solution and O-horizon DOC in several other studies (Solinger et al. 2001; Fröberg et al. 2006), just as we did not find significant seasonal trends in any of our detrital manipulation treatments. However, elevated rates of litter decomposition during months with soil temperatures and soil moisture contents conducive to microbial activity typically increase DOC concentrations relative to the cooler or drier months (Fellman et al. 2009; Laudon et al. 2004). Furthermore, Lajtha et al. (2005) previously found different DOC concentrations at the soil surface between seasons for the DW treatment. We suggest four potential mechanisms to explain why we did not detect seasonal DOC trends:

Table 3 Average DOC concentrations by depth for all treatments + 1 SE

DOC concentration \pm 1 SE (mg/L)						
Depth	CTL	DW	DL	NL	NI	NR
0	35 \pm *	100 \pm *	50 \pm *	–	–	–
10	25 \pm *	69 \pm *	35 \pm *	–	–	–
30	5.3 \pm 0.3	8.4 \pm 0.7	3.7 \pm 0.3	3.2 \pm 0.3	2.9 \pm 0.2	2.8 \pm 0.4
100	2.1 \pm 0.2	2.4 \pm 0.2	2.0 \pm 0.2	2.2 \pm 0.3	1.8 \pm 0.2	1.5 \pm 0.2

Concentrations at 10 cm were calculated from linear interpolation between the surface and 30 cm. The surface concentrations for CTL, DW, DL treatments were from field measurements completed in 2005 (Lajtha et al. 2005). The * symbol denotes that the SE was not available or is unknown, treatments that were statistically different from the control are bolded

Table 4 DOC flux at multiple soil depths for all treatments + 1 SE

DOC flux \pm standard error (g/m ² /year)						
Depth (cm)	CTL	DW	DL	NL	NI	NR
0	73 \pm *	210 \pm *	104 \pm *	–	–	–
10	46 \pm *	130 \pm *	63 \pm *	–	–	–
30	8.3 \pm 0.5	13.1 \pm 1.1	5.7 \pm 0.5	5.0 \pm 0.5	5.9 \pm 0.4	5.7 \pm 0.8
100	2.7 \pm 0.3	3.1 \pm 0.3	2.7 \pm 0.3	2.9 \pm 0.4	3.7 \pm 0.4	3.0 \pm 0.4

Flux was calculated using average DOC concentrations reported in Table 3 and the computed average annual water flux from the Hydrus simulation (Table 2). The * symbol denotes that the SE was not available or is unknown

(1) there may not have been a sufficient sampling frequency to detect change, (2) litter sources were able to sustain a steady DOC production rate in winter despite low temperatures and high rates of water flux, (3) the higher production rate of DOC during summer months was matched by an equal increase in microbial consumption of soluble products, and/or (4) seasonal trends did occur, but were experienced almost entirely in preferential flow paths that were not sampled by the tension lysimeters. We believe that all four mechanisms operating at different time scales could have obscured the presence of seasonal trends. The issue of preferential flow would explain why more studies have been able to describe DOC seasonality in stream water rather than soil solution (Solinger et al. 2001; Fröberg et al. 2006). Preferential flow paths can be a significant pathway for infiltration in forest soils, especially for sandy soils under sustained unsaturated conditions (Kung 1990a, b; Ritsema et al. 1993; Hagedorn and Bundt 2002). There are two pieces of evidence that strengthen the likelihood of this phenomenon at the H.J. Andrews study site: (1) the soils in question have a relatively sandy texture (loam–sandy loam) and (2) the Hydrus model predicted that the soil profile remained unsaturated during all 17 years of our simulation. This suggests that if a preferential flow path was created, it would be persistent throughout the entirety of our study period (Kung 1990a, b).

Temporal trends

We hypothesized that DOC in the removal treatments would decline over time as the most labile microbially-accessible C pools were depleted and not renewed by litter inputs. However, it seems that DOC responded rapidly to the litter treatments, quickly reaching a new steady state for DOC

production instead of gradually changing over annual timescales. After the initial decline in DOC, litter and soil C pools were not then further depleted to cause additional, measurable decreases in DOC annually. While the linear mixed effects model reported no annual trends that met the $p = 0.05$ significance threshold at 30 cm, the NR treatment DOC concentration was close to having a positive linear trend over time. This may indicate that the NR DOC has increased with time at 30 cm, but we had an insufficient sampling frequency in the last ten years to further refine this result. Further research may help to refine and validate this observation.

Detrital treatment effects

Although there was minimal change in DOC concentrations over seasonal and annual timescales for most treatments, mean DOC concentrations at 30 cm were clearly different between treatments (Fig. 1). We hypothesized that DOC concentrations would be greater in the litter addition treatments (DW and DL), but that this could be confounded by priming-induced consumption of high-quality products in the DL treatment. The mean DOC concentration for the DL treatment at 30 cm decreased by 30% relative to the CTL (3.7 versus 5.3 mg C/L) despite higher surface C inputs. This provides strong evidence that priming occurred in the DL plots as hypothesized. Lajtha et al. (2005) reported that DL DOC concentrations in zero-tension lysimeters below the O horizon were approximately 15 mg C/L greater than the CTL treatment after 6 years of litter manipulation. Assuming this input DOC concentration, the rate of DOC consumption was approximately 1.5 times (56%) greater between the surface and 30 cm under the DL treatment relative to the CTL. This accelerated

consumption is greater than the 11.5–34% increase in C loss to respiration from priming reported previously (Sulzman et al. 2005; Crow et al. 2009a, b), although similar in magnitude. Previous studies (Córdova et al. 2018; Sulzman et al. 2005; Crow et al. 2009a, b) have shown that respiration can accelerate more rapidly than carbon assimilation rates when priming occurs, and indeed, SOM stabilization and SOM concentrations have not increased in DL plots compared to control plots. Therefore, the observed priming effect in our study provide evidence that higher input rates of labile C (leaf litter) may not result in higher rates of stable SOC formation, contradicting predictions of the MEMS hypothesis (Cotrufo et al. 2013).

The DW treatment had a mean DOC concentration more than 2 times greater than the DL treatment at 30 cm (8.4 mg C/L vs. 3.7 mg C/L). This suggests that litter comprised of partially decomposed woody debris is more effective at transporting C to deep soil horizons than detritus composed of high-quality leaf and needle litter. DW DOC concentrations at the soil surface were previously measured as ~ 100 mg C/L (Lajtha et al. 2005) which is 65 mg C/L greater than the CTL treatment (Table 3). Like the DL treatment, increased litter inputs accelerated C consumption rates. The rate of DOC consumption was approximately 3-fold greater between the surface and 30 cm under the DW treatment relative to the CTL. Therefore, wood derived DOC was subjected to a greater increase in consumption than the DL treatment. However, DOC concentrations in this treatment were still ultimately greater at 30 cm than the CTL and DL treatments. We believe that the DW treatment led to the highest observed DOC concentration because (1) it had the greatest litter C input and (2) wood derived DOC has a greater proportion of recalcitrant C products that were not metabolized in soil solution because it has a high C:N ratio, a greater proportion of hydrophobic compounds, and can decrease soil solution pH (Spears and Lajtha 2004; Yano et al. 2005).

The lower DOC concentrations in the litter exclusion treatments were consistent with the hypothesis that decreasing C inputs would deplete degradable and soluble C sources and result in reduced DOC production. The litter exclusion treatments (NL, NR, NI) had an average concentration which decreased by 46% relative to the CTL at 30 cm. The elimination of aboveground litter and root C inputs in the NI treatment, had the same effect as eliminating just

one of those factors in the NR and NL treatments. This suggests that the dominant DOC source in these plots was desorption of already stored C products from the soil matrix. Sorption–desorption reactions have been proposed as the dominant mechanism to control soil solution chemistry in subsurface soil horizons previously (Yano et al. 2005; Fröberg et al. 2006). Fröberg et al. (2006) found that DOC chemistry in these horizons was distinct from surface DOC sources, suggesting that the soil matrix itself was the origin of DOC.

Soil solution DOC was effectively homogenized 100 cm belowground between treatments despite 20 years of sustained litter manipulations. This is consistent with the findings of Yano et al. (2005), who suggested that sorption and microbial processing buffered litter treatment effects, as the soil retained as much as 98% of DOC inputs between the surface and 100 cm belowground. Strid et al. (2016) similarly discovered that DOC was chemically homogenous among treatments at 30 cm and 100 cm and Fröberg et al. (2006) found that a majority of DOC in subsurface B-horizons is derived from the horizon itself. These findings broadly suggest that aboveground litter manipulations have little influence on DOC in deeper soil horizons unless sufficient time is given for a change in C storage on mineral binding sites. After 20 years of litter manipulation this has still not occurred, thus we expect such a process requires further time or additional litter inputs for detectable change to occur.

DOC flux

Lysimeter DOC concentrations, coupled with the Hydrus model, revealed that DOC flux into groundwater was small (2.7–3.7 g/m²/year), and relatively negligible compared to the 3.4–8.6 kg C/m² estimated to be stored in the different aboveground litter manipulations at the study site (unpublished). This annual DOC flux accounts for < 0.1% of total litter C and is consistent with the 0.9–13.9 g C/m²/year reported for similar forested catchments by Creed et al. (2008) and the 2.0–3.8 g C/m²/year estimated by Lajtha et al. (2005). Conveyance of DOC into surface horizons was much greater than into groundwater; annual flux was two orders of magnitude higher (73–210 g/m² year) and accounted for 1.4–2.4% of total litter C. This is greater than the 20–35 g/m²/year

previously estimated by Solinger et al. (2001). Therefore, our findings provide support that DOC transport is an important source of C to shallow soil horizons. Detritus with a large proportion of coarse woody debris (DW treatment) was the most effective at conveying C into soils at the surface and in deeper horizons. Thus, decaying wood likely plays an important role in maintaining high soil C concentrations in surface and subsurface soil horizons. This has important implications for forested systems subjected to logging and fuel reduction practices, which generally reduce the prevalence of woody debris.

Our DOC flux estimates assume that preferential flow paths are negligible. As discussed previously, there are a number of factors that make this unlikely, including the sandy soil texture, the thick O-horizon typical at the site (Yano et al. 2005), and model results that indicate sustained unsaturated conditions. Therefore, the actual DOC transport below 100 cm could be much greater than our estimate. Despite having slightly lower concentrations, the NI and NR treatments had the highest rates of DOC flux below 100 cm because annual infiltration was greatest in these plots with the absence of root-water uptake. Therefore, the removal of live root biomass effectively increased C transport from the terrestrial forest ecosystem into groundwater and streams.

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References

- Bates D, Mächler M, Bolker B, Walker S (2014) Fitting linear mixed-effects models using lme4. arXiv preprint arXiv:1406.5823
- Bradford MA, Keiser AD, Davies CA et al (2013) Empirical evidence that soil carbon formation from plant inputs is positively related to microbial growth. *Biogeochemistry* (Dordr) 113:271–281. <https://doi.org/10.1007/s10533-012-9822-0>
- Cleveland CC, Neff JC, Townsend AR, Hood E (2004) Composition, dynamics, and fate of leached dissolved organic matter in terrestrial ecosystems: results from a decomposition experiment. *Ecosystems* 7:175–285. <https://doi.org/10.1007/s10021-003-0236-7>
- Córdova SC, Olk DC, Dietzel RN, Mueller KE, Archontoulis SV, Castellano MJ (2018) Plant litter quality affects the accumulation rate, composition, and stability of mineral-associated soil organic matter. *Soil Biol Biochem* 125:115–124. <https://doi.org/10.1016/j.soilbio.2018.07.010>
- Cotrufo MF, Wallenstein MD, Boot CM et al (2013) The Microbial Efficiency-Matrix Stabilization (MEMS) framework integrates plant litter decomposition with soil organic matter stabilization: do labile plant inputs form stable soil organic matter? *Glob Change Biol* 19:988–995. <https://doi.org/10.1111/gcb.12113>
- Creed IF, Beall FD, Clair TA et al (2008) Predicting export of dissolved organic carbon from forested catchments in glaciated landscapes with shallow soils. *Glob Biogeochem Cycles*. <https://doi.org/10.1029/2008GB003294>
- Crow SE, Lajtha K, Bowden RD et al (2009a) Increased coniferous needle inputs accelerate decomposition of soil carbon in an old-growth forest. *For Ecol Manag* 258:2224–2232. <https://doi.org/10.1016/j.foreco.2009.01.014>
- Crow SE, Lajtha K, Filley TR et al (2009b) Sources of plant-derived carbon and stability of organic matter in soil: implications for global change. *Glob Change Biol* 15:2003–2019. <https://doi.org/10.1111/j.1365-2486.2009.01850.x>
- Daly C (2019) Andrews data catalog. HJ Andrews Experimental Forest Long-Term Ecological Research
- Feddes RA, Kowalik PJ, Zaradny H (1978) Simulation of field water use and crop yield. Center for Agricultural Publishing and Documentation, Wageningen
- Fellman JB, Hood E, D' amore DV et al (2009) Seasonal changes in the chemical quality and biodegradability of dissolved organic matter exported from soils to streams in coastal temperate rainforest watersheds. *Biogeochemistry* (Dordr) 95:277–293. <https://doi.org/10.1007/s10533-009-9336-6>
- Fröberg M, Berggren D, Bergkvist B et al (2006) Concentration and fluxes of dissolved organic carbon (DOC) in three Norway spruce stands along a climatic gradient in Sweden. *Biogeochemistry* (Dordr) 77:1–23. <https://doi.org/10.1007/s10533-004-0564-5>
- Green WH, Ampt GA (1911) Studies on soil physics. *J Agric Sci* 4:1–24. <https://doi.org/10.1017/S0021859600001441>
- Hagedorn F, Bundt M (2002) The age of preferential flow paths. *Geoderma* 108:119–132. [https://doi.org/10.1016/S0016-7061\(02\)00129-5](https://doi.org/10.1016/S0016-7061(02)00129-5)
- Kung K-JS (1990a) Preferential flow in a sandy vadose zone: 2. Mechanism and implications. *Geoderma* 46:59–71. [https://doi.org/10.1016/0016-7061\(90\)90007-V](https://doi.org/10.1016/0016-7061(90)90007-V)
- Kung K-JS (1990b) Preferential flow in a sandy vadose zone: 1. Field observation. *Geoderma* 46:51–58. [https://doi.org/10.1016/0016-7061\(90\)90006-U](https://doi.org/10.1016/0016-7061(90)90006-U)
- Lajtha K, Jarrell WM, Johnson DW et al (1999) Collection of soil solution. In: Standard soil methods for long-term ecological research, vol 2. Oxford University Press, Oxford, pp 166–182
- Lajtha K, Crow SE, Yano Y et al (2005) Detrital controls on soil solution N and dissolved organic matter in soils: a field experiment. *Biogeochemistry* 76:261–281. <https://doi.org/10.1007/s10533-005-5071-9>
- Lajtha K, Bowden RD, Crow S et al (2018) The detrital input and removal treatment (DIRT) network: insights into soil carbon stabilization. *Sci Total Environ* 640–641:1112–1120. <https://doi.org/10.1016/j.scitotenv.2018.05.388>
- Laudon H, Köhler S, Buffam I (2004) Seasonal TOC export from seven boreal catchments in northern Sweden. *Aquat*

- Sci 66:223–230. <https://doi.org/10.1007/s00027-004-0700-2>
- Lee M-H, Park J-H, Matzner E (2018) Sustained production of dissolved organic carbon and nitrogen in forest floors during continuous leaching. *Geoderma* 310:163–169. <https://doi.org/10.1016/j.geoderma.2017.07.027>
- McMinn RG (1963) Characteristics of Douglas-fir root systems. *Can J Bot* 41:105–122. <https://doi.org/10.1139/b63-010>
- Melillo JM, McGuire AD, Kicklighter DW et al (1993) Global climate change and terrestrial net primary production. *Nature* 363:234–240. <https://doi.org/10.1038/363234a0>
- Pan Y, Birdsey RA, Fang J et al (2011) A large and persistent carbon sink in the world's forests. *Science* 333:988–993. <https://doi.org/10.1126/science.1201609>
- R Core Team (2019) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna
- Ritsema CJ, Dekker LW, Hendrickx JMH, Hamminga W (1993) Preferential flow mechanism in a water repellent sandy soil. *Water Resour Res* 29:2183–2193. <https://doi.org/10.1029/93WR00394>
- Schimel D, Melillo J, Tian H et al (2000) Contribution of increasing CO₂ and climate to carbon storage by ecosystems in the United States. *Science* 287:2004–2006. <https://doi.org/10.1126/science.287.5460.2004>
- Schlesinger W (1997) *The biosphere: biogeochemical cycling on land*. Academic, San Diego
- Simunek J, Sejna M, Saito H et al (2013) *The Hydrus-1D software package for simulating the movement of water, heat, and multiple solutes in variably saturated media*. Version 4.17. PC-Progress, Department of Environmental Sciences, University of California Riverside, Riverside
- Solinger S, Kalbitz K, Matzner E (2001) Controls on the dynamics of dissolved organic carbon and nitrogen in a Central European deciduous forest. *Biogeochemistry* 55:327–349. <https://doi.org/10.1023/A:1011848326013>
- Sollins P, Grier CC, McCorison FM et al (1980) The internal element cycles of an old-growth Douglas-fir ecosystem in western Oregon. *Ecol Monogr* 50:261–285. <https://doi.org/10.2307/2937252>
- Spears J, Lajtha K (2004) The imprint of coarse woody debris on soil chemistry in the western Oregon Cascades. *Biogeochemistry* 71:163–175. <https://doi.org/10.1007/s10533-004-6395-6>
- Strid A, Lee BS, Lajtha K (2016) Homogenization of detrital leachate in an old-growth coniferous forest, OR: DOC fluorescence signatures in soils undergoing long-term litter manipulations. *Plant Soil* 408:133–148. <https://doi.org/10.1007/s11104-016-2914-1>
- Sulzman EW, Brant JB, Bowden RD, Lajtha K (2005) Contribution of aboveground litter, belowground litter, and rhizosphere respiration to total soil CO₂ efflux in an old growth coniferous forest. *Biogeochemistry* 73:231–256. <https://doi.org/10.1007/s10533-004-7314-6>
- Yano Y, Lajtha K, Sollins P, Caldwell BA (2005) Chemistry and dynamics of dissolved organic matter in a temperate coniferous forest on Andic soils: effects of litter quality. *Ecosystems* 8:286–300. <https://doi.org/10.1007/s10021-005-0022-9>

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