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Forest harvest legacies control dissolved organic carbon export in small watersheds, western Oregon

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Abstract This study examined physical and biological controls on dissolved organic carbon (DOC) fluxes from conifer-forest watersheds in the H.J. Andrews Experimental Forest of Oregon. We tested how DOC export was related to streamflow and legacies of wood on the forest floor three to five decades after harvest of old-growth forest in seven watersheds spanning the rain to snow elevation gradient. Three watersheds had old-growth forest and four had 30 to 50-year-old forest established after clearcutting of old-growth forest. Mean annual DOC flux in the watersheds was related to the biomass of forest floor wood, which was two or three times higher in watersheds with old-growth forest compared to young forest, and was inversely related to elevation, a measure of snowpack depth and duration. In contrast, fluxes of inorganic elements such as Si and Ca did not vary with harvest history or forest floor characteristics. Annual fluxes of DOC, Si, and Ca were linearly related to annual runoff, and annual volume-weighted concentrations of these ions declined by $< 0.6\%$ with several-fold increases in annual runoff. Across all years, DOC concentrations peaked before the peak of the hydrograph in all watersheds, which we interpret as representing movement, likely via preferential and surficial flow, of organic materials mineralized and solubilized during the long dry summers in this ecosystem. DOC concentrations relative to stream flow exhibited clockwise hysteresis loops in each water year, also suggesting that soluble DOC produced in the dry summer is exported in the fall. DOC concentration differences between reference and harvested watersheds also peaked in late summer or early fall, suggesting that the source of the additional DOC from reference watersheds came from coarse woody debris that remains moist during the dry summers and that was significantly greater in watersheds with elevated DOC. Taken together, our results suggest that forest floor wood is a previously unappreciated control on the supply of DOC that can be exported, and runoff is a secondary control on total DOC flux to streams. The legacy of forest harvest on DOC flux can be observed for decades, as total ecosystem carbon stocks, especially coarse woody debris, may require centuries to develop after old-growth forest harvest.

Keywords Dissolved · Organic carbon · DOC · LTER · Si · Ca · Old-growth forest · Pacific Northwest · H.J. Andrews

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Introduction

Dissolved organic carbon (DOC) export in streams is an important component of the carbon cycle of a watershed (Pacific et al. 2010; Raymond and Saiers 2010) and a critical source of energy for the aquatic food web (Burrows et al. 2013). DOC in streams is the result of many processes, including DOC production from terrestrial sources of carbon (C), decomposition, respiratory losses, sorption, and transport along variable flowpaths within soils, as well as alteration and respiration of DOC within the riparian and stream system. While concentrations of nitrogen (N) in receiving waters have often been used as indicators of N uptake and turnover processes within the terrestrial ecosystem (Likens 2004; Adams et al. 2014; Bernal et al. 2012; Cairns and Lajtha 2005), long-term records of DOC concentrations and fluxes in watersheds are less common. However, changes in DOC flux over time may serve as a sensitive indicator of changes in climate, land management, or terrestrial net primary productivity, or other factors affecting biogeochemical cycling in watersheds (e.g., Sollins and McCorison 1981; Sedell and Dahm 1990; Munn and Meyer 1990).

Many factors have been invoked to explain seasonal trends in DOC fluxes in streams and rivers. The commonly observed rapid increase of DOC concentration on the rising limb of storm hydrographs has been interpreted as a near-stream or in-stream source of DOM (Buffam et al. 2001; Pacific et al. 2010). Wetlands and saturated zones inhibit respiratory losses of DOC, and thus percent wetland cover explained differences in average annual DOC export among watersheds with significant wetland areas (e.g. Eckhardt and Moore 1990; Creed et al. 2008; Larson et al. 2014). Because soil DOC concentrations are generally higher in surface soils than in deep soils due both to sorption and respiration with passage through soil (Yano et al. 2005; Toosi et al. 2014), surficial flowpaths and preferential flow through hillslope soils may be dominant sources of stream DOC in watersheds that have limited wetland/riparian zones (Gannon et al. 2015; Boyer et al. 1997; Bartsch et al. 2013). Hydrological connectivity among flow pathways also influences sources and amounts of DOC exported to streams (e.g. Pacific et al. 2010).

Trends in DOC over larger spatial scales and over time are similarly difficult to attribute to specific drivers. When long-term monitoring stations reported widespread increases in concentrations of DOC in the surface waters of glaciated landscapes across eastern North America and northern and central Europe, various mechanisms were proposed, including climate warming (Monteith et al. 2007). Evans et al. (2006, 2012) used replicated field experiments coupled with long-term observations to demonstrate the trends were more likely due to widespread recovery from acidification, as DOC leaching was previously suppressed by high levels of soil acidity in peat and organo-mineral soils. Other models and observations support the hypothesis that changes in atmospheric deposition were dominant controls on DOC fluxes (e.g. Monteith et al. 2007; Hruška et al. 2009; SanClements et al. 2012; Bragée et al. 2015) and suggested that the observed DOC increases were likely due to declines in ionic strength that resulted from declining atmospheric deposition of both acids and salts.

The role of other climatic factors is less clear, and a relationship with temperature is not expected to be simple. Microbial processing of organic matter increases with temperature, and many studies (Gödde et al. 1996; Christ and David (1996) observed that the production of DOC increased exponentially in moderately wet soils, especially in laboratory incubations. However, others (Kalbitz et al. 2000; Bengtson and Bengtsson 2007) noted that microbial respiration of DOC also increases with temperature, and thus flux of DOC with elevated temperature would be a balance between production and consumption processes that are likely to depend on soil characteristics and soil microbial communities, as well as interactions with soil moisture, and so not readily predictable among different ecosystems. It is thus not surprising that while several studies have observed a relationship between temperature and/or frost and catchment DOC export, others have not, or else results are mixed among streams within a region (Ågren et al. 2010; Creed et al. 2008; Wallin et al. 2015; Hentschel et al. 2009; Hagedorn et al. 2010; Kasurinen et al. 2016).

Land management also affects DOC export and chemistry (Bartsch et al. 2013; Petrone et al. 2011; Williams et al. 2010; Cawley et al. 2014; Yamashita et al. 2011). Conversion of forest to agriculture increased DOC exports to streams or altered DOC chemistry in some cases (Wilson and Xenopoulos 2009), but not in others (Jordan et al. 1997; Larson et al. 2014; Wohlfart et al. 2012; Kindler et al. 2011). Forest harvest also altered the amount and composition of exported DOC in some paired watersheds (Cawley et al. 2014; Yamashita et al. 2011), which has been attributed to post-harvest increases in forest floor litter (Qualls et al. 2000), or post-harvest elevated temperatures (Kalbitz et al. 2004). Other studies have not found changes in DOC export or chemistry after harvest (Burrows et al. 2013; Dai et al. 2001). Potential causes of these discrepancies include differences in geologic or flowpath characteristics, residual forest floor C stocks, or the sorptive properties of the subsoil.

This study examined physical and biological controls on DOC export using an 11-year record of DOC concentrations and fluxes in four pairs of experimental watersheds in the H.J. Andrews Experimental Forest of Oregon. Sites span the rain to snow elevation gradient, and vegetation, precipitation and stream chemistry, hydrology, and climate have been measured since the 1950s and 1960s. We contrasted DOC in watersheds with old-growth Douglas-fir/western hemlock forest to paired watersheds where old-growth forest was harvested in the 1960s or 1970s and replanted with Douglas-fir plantations, at sites in the rain zone, the transient snow zone, and the seasonal snow zone. We hypothesized that DOC export would be reduced in young forests relative to old-growth forests, because of reduced sources of potentially mineralizable and soluble C such as woody and needle debris on the forest floor and a reduction in active roots in soil. Moreover, we expected that the legacy of old-growth forest harvest on DOC flux would last for decades to centuries because ecosystem carbon stocks, especially coarse woody debris, recover on the century scale after harvest (e.g., Gray et al. 2016). We also expected to see a reduction in DOC export at colder (higher elevation) sites, because microbial activity, and thus mineralization of terrestrial detrital C stores, is limited by temperature. However, we also recognized that temperature could increase the in-stream metabolism of any terrestrially-released DOC, thus obscuring any pattern between DOC flux and temperature. In addition, we hypothesized that at the annual time scale, DOC flux from individual watersheds would increase with total stream flow but would show an asymptotic pattern with increasing stream flow as readily soluble organic compounds are depleted over the high-rainfall winters.

Methods

The study examined streamflow and water chemistry in four pairs of treated/reference watersheds located along an elevation gradient in the H.J. Andrews Experimental Forest (122°15′W, 44°12′N) in the Willamette National Forest of western Oregon. Study watersheds range in size from 9 to 96 ha and from 430 to 1100 m in elevation (Table 1). The geology of low-elevation watersheds (WS 1, 2, 9, and 10) is highly weathered Oligocene tuffs and breccias that are prone to mass movements. Upper elevation watersheds (above ~ 800 m, WS 6, 7, and 8) are underlain by Miocene andesitic basalt lava flows (Dyrness 1969; Swanson and James 1975; Swanson and Swanston 1977). Soils are loamy, well-drained, and permeable, with variable depth and rock content (Dyrness 1969; Dyrness and Hawk 1972). Area-averaged slope gradients are > 60% at low elevation (WS 1, 2, 9, and 10) and 30% at high elevation (WS 6, 7, and 8).

Mean daily air temperature ranges from 2 °C (December) to 20 °C (July) at 430 m and from 1 °C (December) to 17 °C (July) at 1300 m. Mean annual precipitation is 2300 mm. More than 75% of precipitation falls between November and April, and actual evapotranspiration averages 45% of precipitation. Study watersheds are located along a gradient of seasonal snow depth and duration (Harr 1981). At high elevation (> 800 m, WS 6, 7, and 8), average snowpack water equivalent (SWE) on April 30 exceeds 700 mm (30% of annual precipitation), and snow may persist for 6 months, whereas at low elevation (< 700 m, WS 9 and 10), snow rarely persists more than 1–2 weeks, and peak SWE is only 2% of precipitation (Harr and McCorison 1979; Harr et al. 1982; Perkins and Jones 2008). Thus, we used elevation as a proxy for snow duration and temperature limitation of microbial activity.

Vegetation of reference watersheds (WS 2, 8, and 9) today, and of the treated watersheds (WS 1, 6, 7, and 10) prior to harvest, was mature and old-growth (150 to > 500-year-old) Douglas-fir/western hemlock forest regenerated after wildfires in the early 1500s and mid-1800s (Weisberg and Swanson 2003; Tepley 2010; Tepley et al., 2013). Overstory canopy cover in the reference watersheds is 70–80%, and leaf area index is > 8 (Dyrness and Hawk 1972; Marshall and Waring 1986; Lutz and Halpern 2006). Vegetation of WS 1, 6, 7, and 10 is Douglas-fir forest that ranged in

Table 1 Basin name (WS = watershed), watershed treatment and forest type, area, elevation range, natural vegetation, harvest treatment and dates, and logging methods for basins used in this study. *Sources* Harr et al. (1979), Rothacher (1965), Harr et al. (1982), Rothacher et al. (1967), Jones and Post (2004)

Basin name	WS 1	WS 2	WS 6	WS 7	WS 8	WS 9	WS 10
Treatment, forest type[a]	Plantation, 40–50 years	Old-growth reference	Plantation, 30–40 years	Plantation, 30–40 years	Old-growth reference	Old-growth reference	Plantation, 30–40 years
Area (ha)	95.9	60.7	13	15.4	21.4	9	10
Elevation range (m)	460–990	530–1070	863–1013	908–1097	955–1190	425–700	425–700
Natural vegetation[b]	450 to 500-year–old Douglas-fir forest	450 to 500-year–old Douglas-fir forest	130 to 450-year old Douglas-fir forest	130 to 450-year old Douglas-fir forest	130 to 450-year old Douglas-fir forest	130 to 450-year old Douglas-fir forest	130 to 450-year old Douglas-fir forest
Treatment, date[c]	100% clearcut 1962–1966; broadcast burn 1966	Reference for WS 1	Roads; 100% clearcut 1974; broadcast burn 1975	Roads 1974; 60% shelterwood cut 1974; remaining overstory cut 1984; broadcast burn lower half of WS 1975; 12% basal area thin 2001	Reference for WS 6, 7	Reference for WS 10	100% clear-cut 1975; no burn
Logging method	100% skyline yarded	–	90% high-lead cable-yarded; 10% tractor yarded	40% high-lead cable-yarded; 60% tractor yarded	–	–	100% high-lead cable-yarded

[a]Age of forest during the study period (2004–2015)

[b]Estimated age of forest in the 1950s and 1960s when experimental watersheds were established

[c]Broadcast burns were controlled burns over the cut area intended to consume logging debris

age from 30 to 50 years over the study period (Perry and Jones 2017).

Each study watershed has continuous streamflow records since November 1952 (WS 1, 2, and 3), November 1963 (WS 6, 7, and 8), or November 1968 (WS 9 and 10) using trapezoidal flumes, to which V-notch weirs are attached in summer months to improve precision of lowflow measurements (Perry and Jones 2017). Nutrient chemistry sampling for all variables except DOC began in October 1968 at WS 9 and 10, October 1971 at WS 6, 7 and 8, June 1981 at WS 2, and June 2003 at WS 1. DOC sampling began in 2004 at all study watersheds. Streamwater is sampled just above the flume at the outlet of each watershed with flow-proportional water samplers, which account for changes in concentration with discharge (Fredriksen 1969). Carboys are collected once a week, refrigerated, and combined at three-week intervals for chemical analysis.

Stream water samples are passed through pre-ashed GF/F (0.7 µm pore size) filters in the laboratory prior to analysis. DOC concentrations are measured using a Shimadzu TOC-VCSH Analyzer; the laboratory determined method detection limit is 50 µg L^{-1}. DOC fluxes were calculated by multiplying the flow-weighted 3-weekly DOC concentrations by discharge.

We used long-term records of Si and Ca in order to compare trends in DOC fluxes with trends in inorganic elements across all watersheds. Silicate in stream water is analyzed by automated colorimetric analysis using a Technicon Auto-Analyzer II; method detection limit is 0.10 mg L^{-1} as silica (Si). Calcium (Ca) is analyzed using flame atomic absorption spectrometry with a Shimadzu AA-7000F FAAS; method detection limits are 0.06 mg L^{-1} for Ca.

In order to examine effects of forest floor woody detritus on DOC fluxes, we used data on live and dead wood biomass that was sampled in all watersheds in the early 2000s in circular, fixed area (0.1 ha) permanent vegetation study plots (Harmon and Sexton 1996, Fasth et al. unpublished data). At all watersheds except WS 2, the volume of logs and fine woody debris and the mass of sample cores of forest floor were measured along four 25-m transects radiating in cardinal directions from the center of each 0.1-ha plot (Fasth et al. unpublished data). In WS 2, log volume instead was calculated from field measurements of diameter and length of every log in each plot. Logs were defined as wood pieces with a diameter > 10 cm; fine woody debris as wood pieces with a midpoint diameter ranging from 0.5 to 10 cm; and forest floor litter biomass as organic matter < 0.5 cm diameter (Fasth et al. unpublished data). Biomass was determined by multiplying by a species- and decay class-specific density (for logs) or measured densities (fine wood) (Fasth et al. unpublished data). For this study, forest floor wood was calculated as the sum of fine woody debris, logs, and forest floor biomass (Table 2).

To test for hysteresis, stream chemistry data (concentrations of DOC, Si, and Ca) at 3-weekly time scales were plotted against 3-weekly discharge. Data were analyzed using ordinary least squares models (Data Analysis package in Excel v. 15.33), following appropriate transformations of variables to meet assumptions of independence and normal distributions. Models were fitted using data at inter-annual and annual time scales. At the inter-annual time scale, mean annual DOC flux (response variable, n = 7 watersheds) was related to forest floor wood (predictor variable from Table 2), and residuals from this model were related to mean elevation, a proxy for winter snowpack duration and soil temperature of each study watershed. At the annual time scale, models were fitted to annual DOC fluxes (response variable, n = 11 years) as a function of annual streamflow (predictor variable), and residuals from this model (response variable) were related to annual winter temperature and suspended sediment (predictor variables). The significance of relationships was assessed based on the p value of the slope term and variance explained. The significance of the differences between reference and treated watersheds was determined by comparing confidence intervals around the slope terms in regression models of annual data.

Results

Woody biomass on the forest floor in the study sites ranged from 62 to 184 Mg ha^{-1} (Table 2). Logs and fine woody debris accounted for the largest differences in total forest floor carbon (Table 2). Because logging methods in WS 1 left behind large amounts of wood, log biomass in WS 1 (young forest) was 70% of log biomass in WS 2 (old growth), whereas log biomass was only 25–35% in WS 6, 7 and 10 (young forest) of log biomass in WS 8 and 9 (old growth) (Table 2).

Table 2 Total biomass of wood (Mg ha^{-1}) by watershed in the Andrews Forest as of the early 2000s

	WS 1	WS 2	WS 6	WS 7	WS 8	WS 9	WS 10
Forest type and age	40–50 year old forest plantation	Old-growth reference for WS 1	30–40 year old forest plantation	30–40 year old forest plantation	Old-growth reference for WS 6,7	Old-growth reference for WS 10	30–40 year old forest plantation
Total biomass (Mg ha^{-1})	267	894	191	130	906	791	232
Of which							
Live tree	142	654	110	55	652	585	134
Understory	9	2	4	10	2	5	8
Snag/stump	13	75	3	3	69	42	17
Fine woody debris	7	10	6	10	11	8	6
Forest floor	24	50	34	23	57	43	37
Logs	72	103	33	29	115	108	29
Total forest floor wood	104	163	74	62	184	159	72
DOC concentration (mg L^{-1})	1.3 ± 0.03	1.6 ± 0.05	0.6 ± 0.03	0.6 ± 0.02	1.2 ± 0.04	2.0 ± 0.05	1.1 ± 0.03
Annual DOC flux (kg $ha^{-1}year^{-1}$)	17 ± 3	16 ± 3	7 ± 2	6 ± 1	13 ± 3	22 ± 5	14 ± 2
Annual flux as % of TEC	0.005	0.001	0.003	0.004	0.001	0.002	0.005

WS 2, 8, and 9 are reference watersheds with 150 to 500-year-old Douglas-fir/western hemlock forests. WS 1, 6, 7, and 10 are Douglas-fir forests established after clearcutting of old-growth forest in the mid 1960s to mid 1970s. Total forest floor wood = fine woody debris + logs + forest floor. DOC values are annual means plus/minus standard deviations for water years 2004–2005 through 2014–2015. *Sources* Fasth and others (unpublished data)

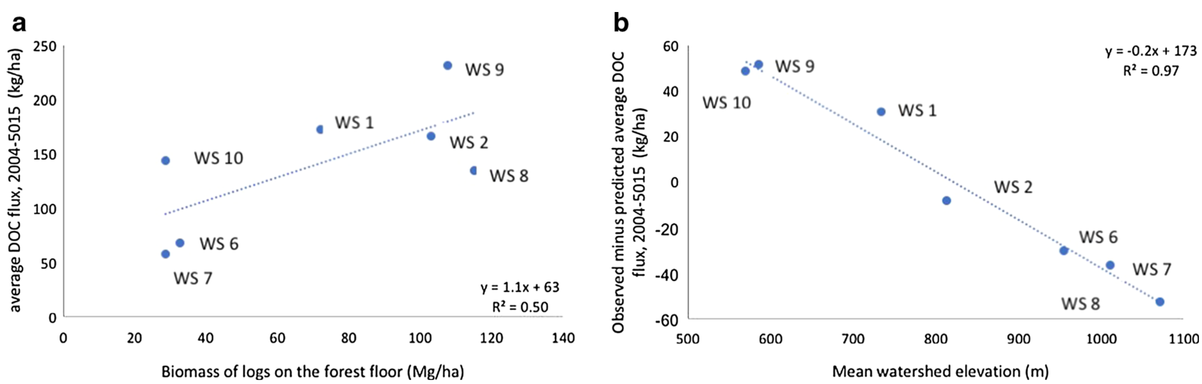


Fig. 1 **a** Average annual DOC flux (kg/ha) as a function of biomass of logs on the forest floor and **b** residual (observed minus predicted) average annual DOC flux as a function of median watershed elevation in seven watersheds in the HJ Andrews Experimental Forest, Oregon. See Table 1 for watershed descriptions and Table 2 for wood biomass data

Annual DOC export is less than 0.005% of total ecosystem carbon, and less than 0.02% of the biomass of wood on the forest floor. Average annual DOC flux was significantly positively related to the biomass of logs on the forest floor (adjusted $r^2 = 0.42$, $p < 0.07$, Fig. 1a) and positively, but not significantly, related to

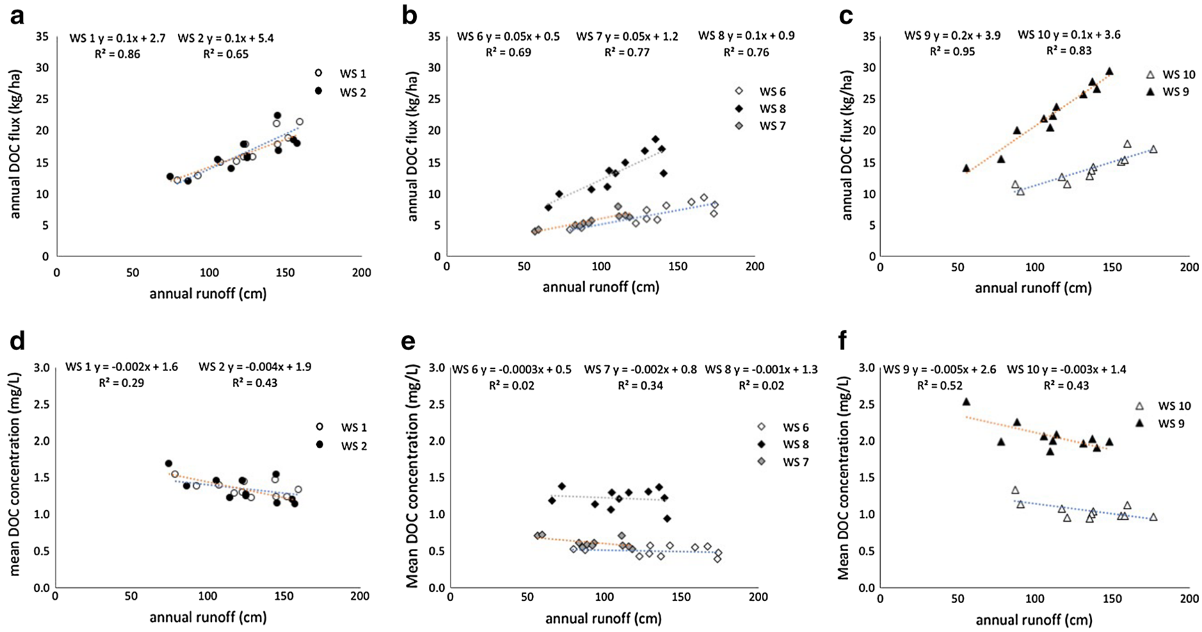


Fig. 2 Annual DOC flux (kg/ha) (**a–c**) and mean DOC concentration (mg L^{-1}) (**d–f**) as a function of annual runoff (cm) for water years 2004 through 2014 (Oct to Sep) in seven watersheds in the HJ Andrews Experimental Forest, Oregon. WS 2, 8, and 9 are reference watersheds with 150 to 500-year-old Douglas-fir/western hemlock forests and WS 1, 6, 7, and 10 are Douglas-fir plantations established after clearcutting of old-growth forest in the mid 1960s to mid 1970s

total forest floor wood biomass ($p < 0.11$). The relationship is primarily driven by the difference between the old-growth reference watersheds (WS 2, 8 and 9) and young forest watersheds (WS 6, 7, and 10); WS 1 was intermediate. DOC flux was independent of elevation, but the residuals from the relationship of DOC flux and forest floor wood were significantly negatively related to elevation (adjusted $r^2 = 0.9$, $p < 0.0007$) (Fig. 1b). Almost all of the variation in mean annual DOC is explained by the combination of forest floor logs and elevation: this means that, after log biomass is accounted for, DOC export is lower at higher elevation.

Annual DOC flux in each small watershed was significantly positively related to annual runoff ($p < 0.003$, Fig. 2a–c). Annual fluxes of Si and Ca also were significantly related to total annual runoff ($p < 0.0001$, Fig. 3a, b). Volume-weighted mean annual concentrations of DOC declined over the observed range of annual runoff by 0.03% (WS 6) to 0.5% (WS 10) (Fig. 2d–f). Si and Ca concentrations decreased by less than 0.2% and 0.6%, respectively, over the observed range of annual runoff (Fig. 3c, d).

In three of the four watershed pairs, DOC flux per unit runoff was significantly lower in the watershed with young forest compared to the reference watershed with old-growth forest (95% confidence intervals for slope terms were 0.23–0.68 and 0.28–0.67 for WS 6 and 7 [young forest], versus 0.65–1.61 for WS 8 [old forest]; they were 0.50–1.02 for WS 10 [young forest] versus 1.39–1.94 for WS 9 [old growth]) (Fig. 2b, c). However, fluxes of DOC were not significantly different in WS 1 (young forest) compared to WS 2 (old-growth forest) (Fig. 2a). Moreover, the increase in DOC flux per unit increase in runoff was significantly greater at the lowest elevation watersheds (WS 9 and 10) compared to higher elevation watersheds (WS 1 and 2, WS 6, 7 and 8, Table 1, Fig. 2a–c). Si and Ca flux did not differ between watersheds with young versus old-growth forest (Fig. 3a, b). Annual fluxes of N and sediment were not related to annual runoff or forest vegetation age (data not shown).

Residuals of the relationship between annual DOC flux and annual runoff (from Fig. 2) were similar over time for watershed pairs. However, they were not significantly related to measures of temperature, including mean annual temperature, summer mean temperature, coldest or warmest three-week interval, or winter temperature. Residuals of annual DOC flux were not related to measures of storminess, including

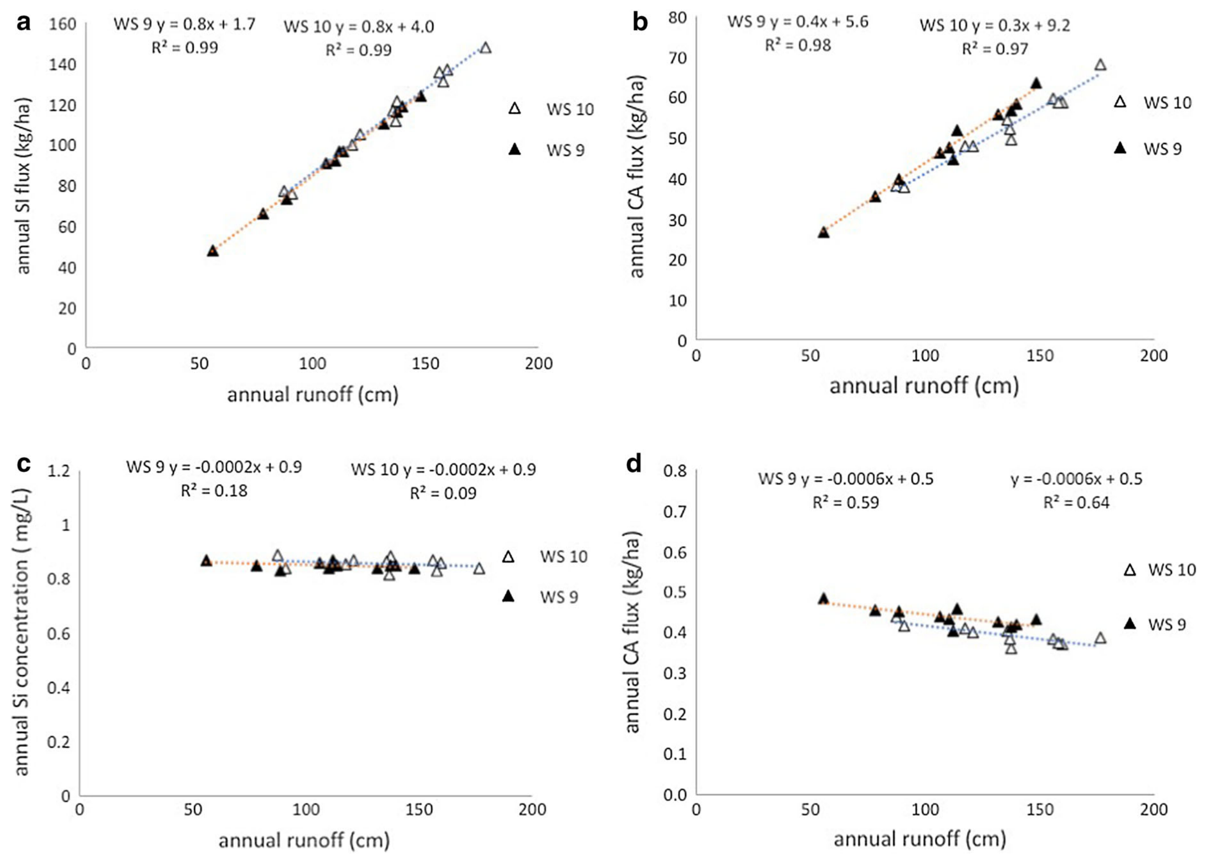


Fig. 3 Annual flux (kg ha^{-1}) (**a**, **b**) and mean concentration (mg L^{-1}) (**c**, **d**) of Si (**a**, **c**) and Ca (**b**, **d**) as a function of annual runoff (cm) for water years 2004 through 2014 (Oct to Sep) in WS 9 and 10 in the HJ Andrews Experimental Forest, Oregon. WS 9 is a reference watershed with 150 to 500-year-old Douglas-fir/western hemlock forests and WS 10 is a Douglas-fir plantation established after clearcutting of old-growth forest in the mid 1970s. Data are shown for WS 9 and 10 only, but these patterns were observed in all watersheds in all years

CV of runoff or maximum daily flow or suspended sediment (data not shown).

DOC concentrations in all watersheds and in all years exhibited clockwise hysteresis loops over the course of the water year (Fig. 4a, d). DOC concentrations are highest at the start of the water year and lowest in the early spring. In contrast, fluxes of Si and Ca showed a mix of classic dilution with near chemostatic behavior over the water year with no hysteresis loops in any watershed or in any year (Fig. 4b, c, e, f).

The concentration of Si and Ca was highest during the dry summer months in all watersheds in all years (Fig. 5). In contrast, the concentration of DOC was highest during the late fall period of hydrograph rise prior to the peak three-weekly discharge (Fig. 6). The greatest difference in concentrations between old-growth and young forest occurred at the time of highest concentrations, before the peak in the hydrograph but at the end of the long dry summer period.

Discussion

In ecosystems with limited areas of peat or wetlands, DOC is only a small component of total ecosystem C flux, and respiration and sediment transport fluxes of C are significantly larger. Argerich et al. (2016), for example, found that at least twice as much C was mobilized in sediment transport in streams as DOC in WS1 of our study site, and that 27% of all C exported by the stream was lost as evasion to the atmosphere. Similarly, DOC flux to streams was only 0.5% of respiration losses from soils in an old-growth plot in

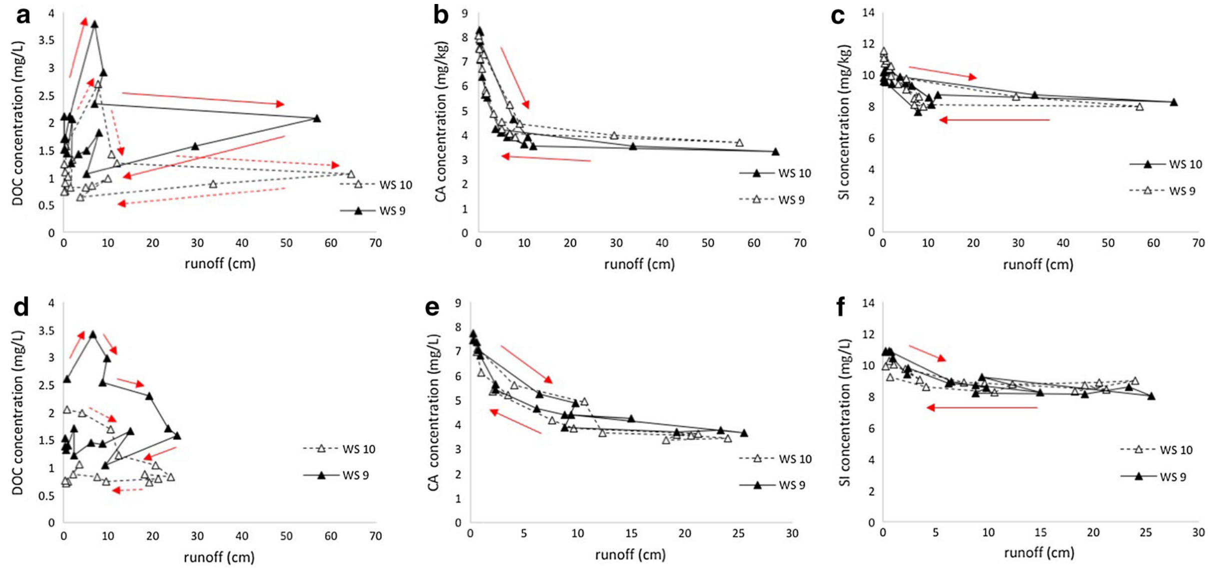


Fig. 4 Three-weekly concentrations (mg L^{-1}) as a function of runoff for **a**, **d** DOC, **b**, **e** Ca, **c**, **f** Si, in October 2005 to September 2006, a year with a few large winter storm events (**a**–**c**) and October 2007 to September 2008, a year with many small winter storm events (**d**–**f**) in WS 9 (old-growth forest) and WS 10 (30 to 40-year-old forest) in the HJ Andrews Experimental Forest, Oregon. Data are shown for WS 9 and 10 for only 2 years, but these patterns were observed in all watersheds in all years

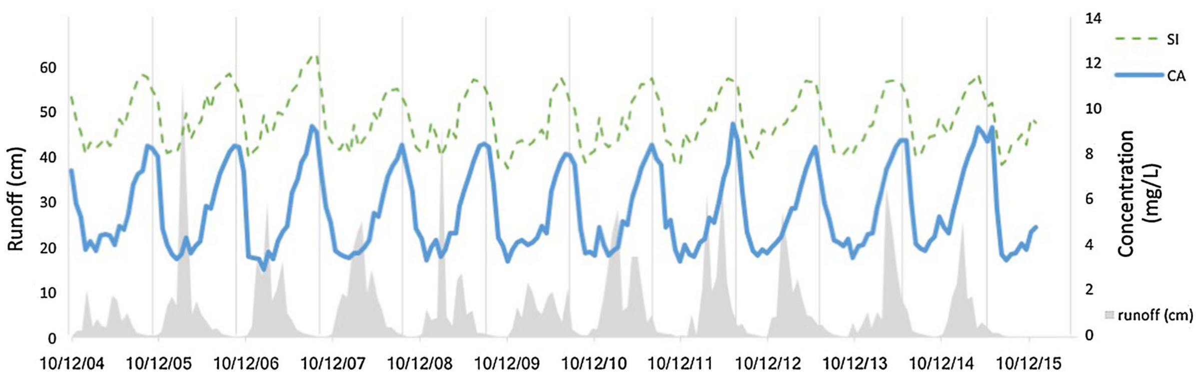
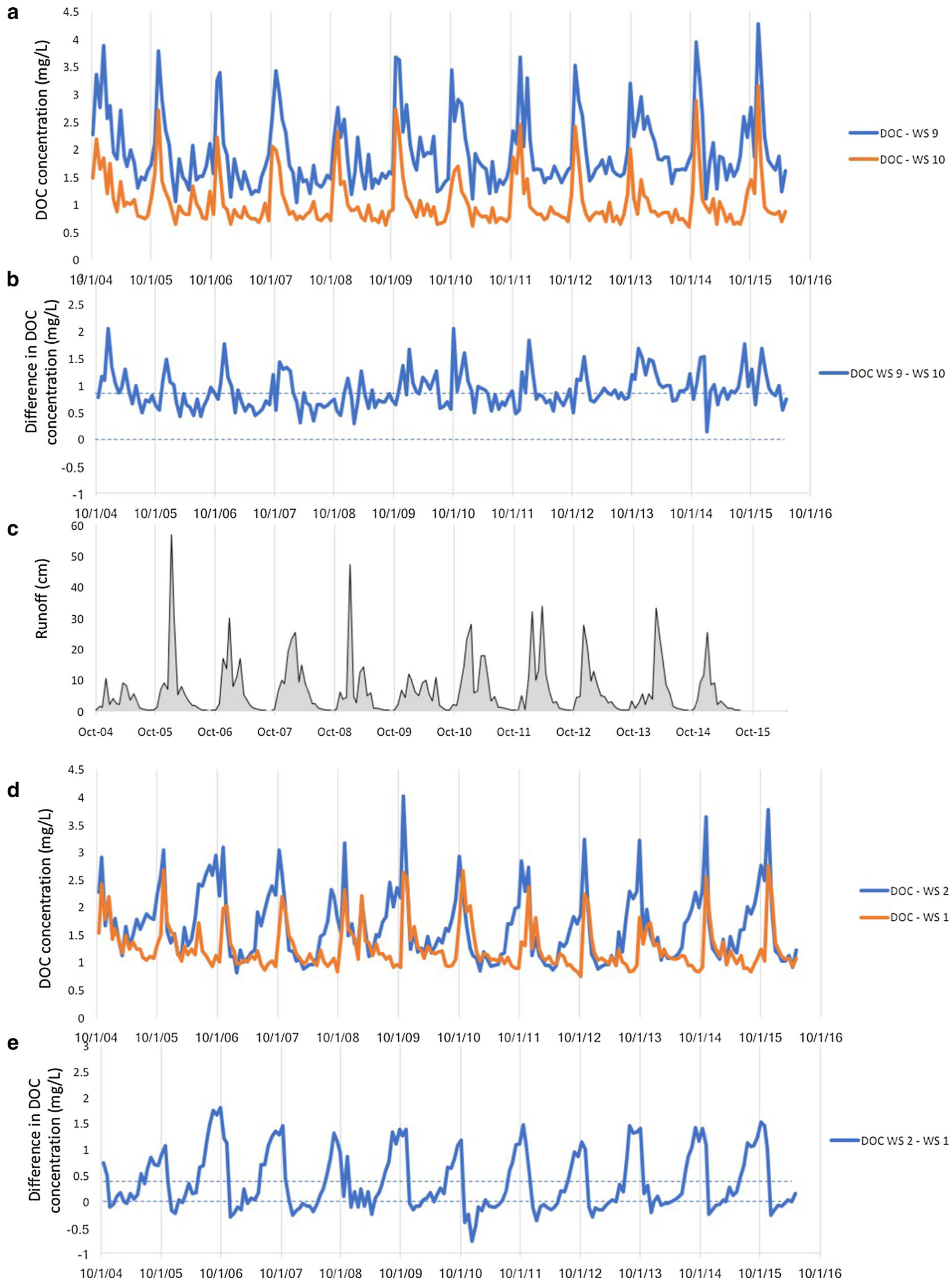


Fig. 5 Three-weekly concentrations for Si and Ca (mg L^{-1}) (right axis) and three-weekly runoff (cm) (left axis) from October 2004 to September 2015 in WS 9 (old-growth forest) in the HJ Andrews Experimental Forest, Oregon. Data are shown for WS 9 only, but these patterns were observed in all watersheds in all years

the Andrews Forest (Lajtha et al. 2005). However, while not a significant component of the overall C budget from the terrestrial ecosystem, DOC is a critical component of stream ecosystem carbon dynamics, as it affects stream metabolism, the balance between autotrophy and heterotrophy, stream acidity, nutrient uptake and bioavailability of many toxic compounds (Stanley et al. 2012). DOC fluxes may also serve as sensitive indicators of forest dynamics within the terrestrial system (e.g. Cawley et al. 2014; Lee and Lajtha 2016), changes in the metabolism of streams, and more regional changes in climate or atmospheric processes due to both natural and anthropogenic drivers. Thus, understanding controls on DOC fluxes from different ecosystems is critical to the interpretation of effects of global change on ecosystem processes.


a
DOC concentration (mg/L)
DOC - WS 9
DOC - WS 10
b
Difference in DOC concentration (mg/L)
DOC WS 9 - WS 10
c
Runoff (cm)
d
DOC concentration (mg/L)
DOC - WS 2
DOC - WS 1
e
Difference in DOC concentration (mg/L)
DOC WS 2 - WS 1

◀ **Fig. 6** Three-weekly concentrations for **a**, **d**, **g** DOC (mg L^{-1}) in old-growth forest and 30 to 40-year-old forest, **b**, **e**, **h** difference in DOC concentration, old forest minus old young (mg L^{-1}), and **c**, **f**, **i** 3-weekly runoff (cm) in old forest reference from October 2004 to September 2015 in the HJ Andrews Experimental Forest, Oregon. **a–c** WS 9 (old forest) and WS 10 (young forest); **d–f** WS 2 (old forest) versus WS 1 (young forest); **g–i** WS 8 (old forest) versus WS 6 (young forest). The horizontal dashed lines in (**b**, **e**, **h**) are at zero (lower line) and the average difference, old forest minus young forest (upper line)

The linear relationship between DOC flux and annual runoff in all watersheds was counter to our initial hypothesis that DOC would decline during periods of high streamflow and low temperatures, when flushing of DOC was expected to exceed DOC production. Although anything but perfect dilution implies an increase in element flux with increasing runoff, we did expect to see asymptotic behavior in years with very high annual streamflow. Linear relationships between solute concentration and watershed runoff imply a chemostatic response, which is commonly observed for inorganic ions on storm and on inter-annual timescales (Godsey et al. 2009), because hydrologic flushing of subsurface materials can increase reactive mineral surface area and stimulate mineral weathering rates (Clow and Mast 2010). In this study, DOC and all cations displayed near-chemostatic behavior, with only small decreases in annual mean volume-weighted concentrations with a several-fold increase in annual streamflow.

Although we found a linear relationship between DOC flux and runoff in all watersheds on an annual timescale, concentrations of DOC exhibited clockwise hysteresis on seasonal time scales. Ca and Si concentrations did not exhibit hysteresis behavior, even though they were highest in summer during baseflow conditions. Clockwise hysteresis may imply that flushing depletes labile and soluble C substrates (Xu et al. 2012; Strohmeier et al. 2013). Alternatively, clockwise hysteresis loops on a seasonal scale may be due to hydrologic flowpaths. Early wet season or storm quickflow and surficial flow water tends to have higher DOC concentrations than baseflow, because DOC is efficiently metabolized with passage through soil (Lajtha et al. 2005; Bengtson and Bengtsson 2007). Large increases in DOC during 3-week periods of high flow were balanced at an annual timescale with periods of decreased DOC flushing. Thus, we found no evidence of source depletion that would cause a deviation from the linear relationship between DOC export and annual runoff.

What could account for the observed lack of an upper bound asymptote in the relationship between runoff and DOC export? We suggest that the high density and legacy of forest floor wood in our study site leads to a relatively steady source of DOC. Smithwick et al. (2002) found that C densities—which include both vegetation and soil C stores—were higher in old-growth forests of the Pacific Northwest than for any other type of vegetation around the world. Mild fall and winter conditions promote high annual net primary production, and accumulation of carbon in live trees and on the forest floor is enhanced by infrequent natural disturbance (long fire return intervals) in old-growth conifer forests of the Pacific Northwest (Harmon et al. 1986; Weisberg and Swanson 2003). The highest rates of large wood inputs to the forest floor occur in old-growth conifer forests in western North America, and conifer forests generally produce more forest floor wood than deciduous forests (Harmon et al. 1986). We hypothesize that the large pool of woody detritus in our forests produces a source of DOC that is moderately resistant to microbial decay and thus can be measured in stream water. Data from the nearby Detrital Input and Removal (DIRT) plots that experimentally manipulate sources of litter to the forest have shown that additions of wood to the forest floor result in significantly elevated DOC levels that can persist for decades (Lajtha et al. 2005). In addition, laboratory experiments have shown sustained rates of DOC release from forest floor materials coupled with a rapid replenishment of DOC pools after leaching (Lee et al. 2018). These results suggest that high loads of potentially leachable C in these forests may sustain the supply of DOC that can be exported to streams, causing the lack of a decrease in DOC production with increasing water flux. These high loads of potentially leachable materials compared to annual DOC flux may also explain the near-chemostatic nature of DOC in this system: during high flow periods, when flow is concentrated near the surface, DOC can be produced and transported to streams without depletion or consumption that would occur in deeper flow paths.

We initially hypothesized that DOC export would be reduced in harvested forests due to the removal of sources of potentially mineralizable and soluble C such as woody and needle debris on the forest floor.

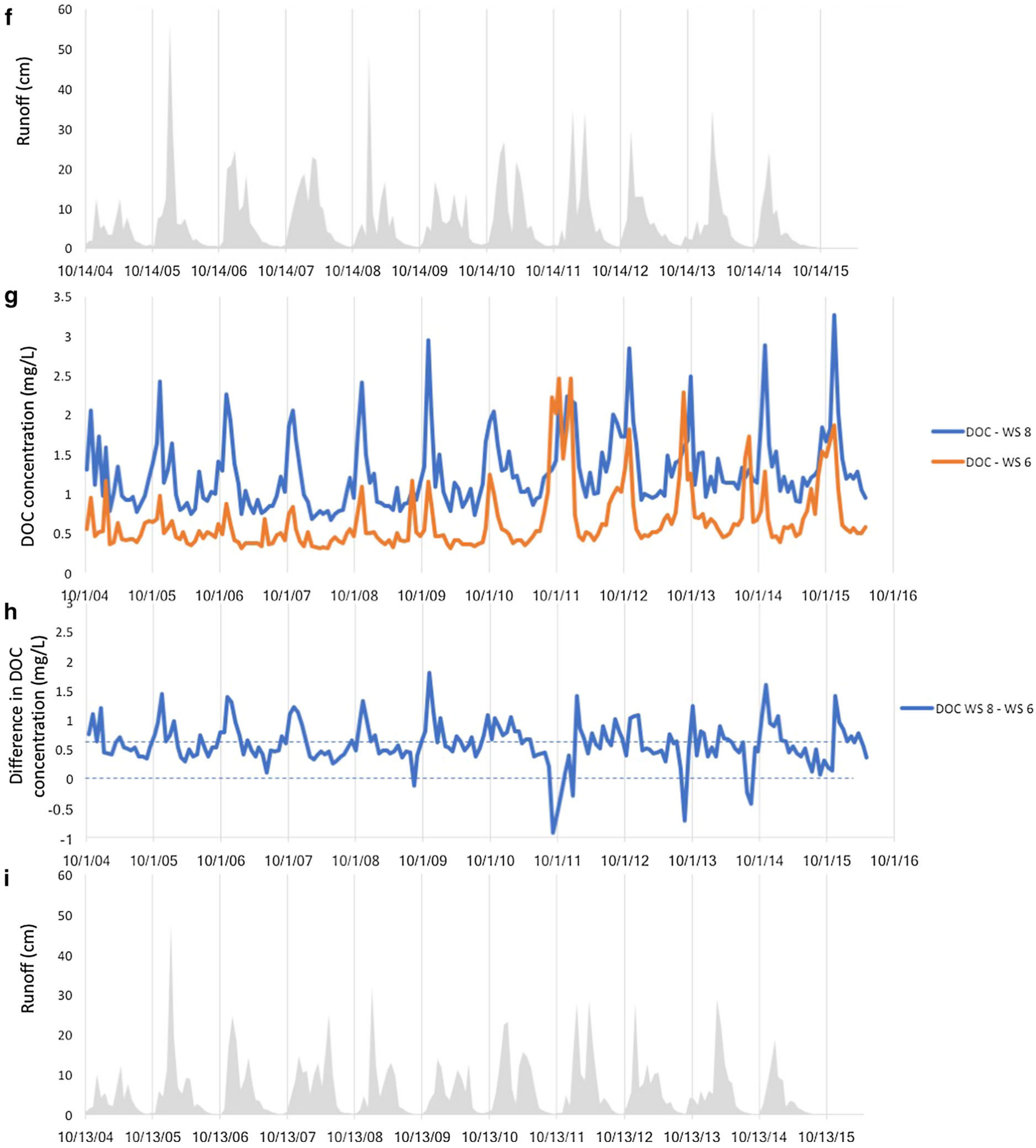


Fig. 6 continued

DOC export was indeed reduced in harvested watersheds compared to their reference old-growth watersheds with the exception of the harvested WS 1, which had an unusually high load of remaining woody debris after harvest. We also predicted that the legacy of old-growth forest harvest on DOC flux would last for decades to centuries because ecosystem carbon stocks, especially coarse woody debris, recover on the century scale after harvest. Indeed, old growth Pacific Northwest forests may continue to accumulate C in vegetation for up to 400 years (Gray et al. 2016). In addition, because forest harvest removes larger trees that otherwise would become decaying logs on the forest floor, forest floor wood is greater in unmanaged than in managed forests (Duvall and Grigal 1999). Patterns of forest floor wood in western Oregon reach a minimum at 80–120 years after disturbance (Spies et al. 1988), consistent with our finding of significantly less coarse woody debris in all but one of our harvested watersheds compared to the reference watersheds, and with our finding of more coarse wood in low-elevation reference watersheds (WS 2, 9) compared to the high-elevation reference watershed (WS 8), which experienced moderate-severity fire in the mid 1800s. Although forest harvest reduces inputs of wood to the forest floor it does not significantly affect soil organic matter stocks unless the harvest is repeated and intensive (Nave et al. 2010; Achat et al. 2015). We did not measure SOM pools in our watersheds, but given the long intervals between fires and the single harvest of the watersheds, we did not expect significant differences in the SOM pools between reference and harvested watersheds. Thus, we argue that the observed differences in DOC export from young (30 to 50-year-old) versus old-growth forest in 3 of our 4 watershed pairs are likely due to differences in forest floor wood, rather than to differences in SOM content.

We were initially surprised by the lack of difference in DOC flux between WS 1, which was harvested in 1962–1966 and had significantly lower live biomass, and WS 2, its old-growth reference watershed. We argue that similar DOC fluxes from WS 1 and WS 2 are due to the fact that WS 1 retained 70% of the forest floor volume of the old-growth forest and that leaching of this forest floor material is a significant contributor to total DOC flux. Indeed, the chemistry of DOC in harvested and reference watersheds support this conclusion. In a study using optical properties of DOC to analyze chemical fingerprints and origin of DOC fluxes, Lee and Lajtha (2016) found that old-growth watersheds and WS1 had significant components of surficial, vegetation-derived DOC. In contrast, 3 of the 4 harvested watersheds (WS 6, 7, 10) had DOC signatures that more closely resembled deeper soil C pools without the strong vegetation signal. However, WS 1, with its higher coarse woody detritus loads, had optical signatures that resembled the other old-growth forests. Taken together, these findings support the hypothesis that wood biomass on the forest floor influenced both DOC chemistry and patterns of DOC flux in this study. However, in forests of the eastern US that have experienced repeated harvest, forest floor wood volume is lower, and the relative contribution of forest floor wood versus soil organic matter to DOC flux is likely significantly smaller, and thus our results are not likely to be generalizable across all forests.

Relative to the ecosystem C budget for the forest, DOC export represents only a small proportion of potentially mobilizable C. In the DIRT plots, the ratio between respiration losses from soil surface and DOC mobilized to deep soil horizons was measured as ∼ 200 (Lajtha et al. 2005), indicating that 0.5% of mobilized C was lost as DOC to streams. Moreover, Spears and Lajtha (2004) found that while DOC concentrations in leachate from logs on the forest floor approximated 100 mg C L^{-1}, mean 3-weekly concentrations of DOC in our streams ranged from 0.6 mg C L^{-1} (WS 7) to 2.0 mg C L^{-1} (WS 9), also indicating that only about 0.5% of mobilized forest floor C reaches streams. However, during high flow periods, DOC transport may increase relative to respiratory loss, contributing to the near-chemostatic behavior of DOC observed in this study. Because DOC is subject to lower sorption and microbial processing during these high flow periods as demonstrated by the optical signatures of DOC observed by Lee and Lajtha (2016), DOC flux is expected to be higher in forests with greater loads of forest floor source materials, as was observed in this study.

Other factors not measured in this study may contribute to the observed differences in DOC flux. Tree biomass is significantly greater in reference watersheds, which likely translates into greater fine root production and turnover as well as greater root exudation. Root exudation can be a significant source of C to soil, and represented 2.5% of NPP in a mixed deciduous forest in Indiana (Yin et al. 2014). However, root exudates, and rhizodeposition in general, have mineralization times of hours to days (Dennis et al. 2010). Although these rhizodeposits may not directly reach streams, they can either be sequestered as new soil C or increase decomposition of more recalcitrant soil C (i.e., priming) through changes in the activity and relative abundance of microbes (Kuzyakov et al. 2000; Fontaine et al. 2004; de Graaff et al. 2010), and thus could influence DOC production. Forest roads, forest harvest, and subsequent decay of roots, increased annual water flux and peak flows in the study watersheds (Jones and Grant 1996), but these effects would tend to increase DOC flux in harvested stands and thus counteract, rather than explain, differences observed in this study.

In this study, controlling for biomass of forest floor logs, average annual DOC flux was lower than expected in upper-elevation watersheds, which have significantly lower air temperature and longer snowpack duration (Jones and Perkins, 2010). This finding suggests that annual DOC flux in streams may be significantly affected by temperature limitations during seasons when terrestrial production of DOC is limited. Seasonal and annual DOC flux is related to air temperature in boreal or peat-dominated landscapes (Köhler et al. 2008; Prokushkin et al. 2005), perhaps due to freeze–thaw disruption of cells and soil structure followed by snowmelt (Ågren et al. 2010). However, soil freezing is very rare in the Andrews Forest study site; thus, we infer that low temperature limits DOC production during winter in this region, when stream metabolism and DOC uptake are not counteracting factors.

Taken together, our results suggest that forest floor wood is a previously unappreciated control on the supply of DOC that can be exported, and runoff is also a significant control on total DOC flux to streams. This study indicates that in old-growth forests of the Pacific Northwest, the very high wood biomass on the forest floor provides a steady source of DOC in proportion to annual precipitation. However, in 30 to 50-year-old forests, where the forest floor woody biomass has been greatly reduced relative to the old-growth forests they replaced, the depletion of forest floor woody biomass produced a substantial decline in DOC export. These findings indicate that the wood on the forest floor plays a hitherto largely unrecognized role in regulating DOC export from forested ecosystems.

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