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Linking aboveground net primary productivity to soil carbon and dissolved organic carbon in complex terrain

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[1] Factors influencing soil organic matter (SOM) stabilization and dissolved organic carbon (DOC) content in complex terrain, where vegetation, climate, and topography vary over the scale of a few meters, are not well understood. We examined the spatial correlations of lidar and geographic information system-derived landscape topography, empirically measured soil characteristics, and current and historical vegetation composition and structure versus SOM fractions and DOC pools and leaching on a small catchment (WS1) in the H.J. Andrews Experimental Forest, located in the western Cascades Range of Oregon, USA. We predicted that aboveground net primary productivity (ANPP), litter fall, and nitrogen mineralization would be positively correlated with SOM, DOC, and carbon (C) content of the soil based on the principle that increased C inputs cause C stores in and losses from in the soil. We expected that in tandem, certain microtopographical and microclimatic characteristics might be associated with elevated C inputs and correspondingly, soil C stores and losses. We confirmed that on this site, positive relationships exist between ANPP, C inputs (litter fall), and losses (exportable DOC), but we did not find that these relationships between ANPP, inputs, and exports were translated to SOM stores (mg C/g soil), C content of the soil (% C/g soil), or DOC pools (determined with salt and water extractions). We suggest that the biogeochemical processes controlling C storage and lability in soil may relate to longer-term variability in aboveground inputs that result from a heterogeneous and evolving forest stand.

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1. Introduction

[2] Soil is the largest terrestrial carbon (C) store, holding a global estimate of approximately 2100 Gt C when quantified by geospatial models [*Ruesch and Gibbs*, 2008; *Post and Kwon*, 2000; *West and Post*, 2002]. Worldwide, the majority of soil C is stored in tropical-subtropical forest, where vegetation inputs are largest, and boreal-tundra grassland soils, where decomposition is slowest [*Amundson*, 2001; *de Deyn et al.*, 2008; *Mahli et al.*, 1999, 2006; *Post and Kwon*, 2000]. Terrestrial C may also be stored in solution in the soil in the form of dissolved organic carbon (DOC). DOC is a product of litter and fine root decomposition and is the critical substrate for microbial respiration; C which is not consumed by microbes moves downward in the soil profile to the mineral layers [*Kalbitz and Kaiser*, 2003; *Marschner and Kalbitz*, 2003; *Sanderman and Amundson*, 2004] and may play a critical role in soil organic matter (SOM) stabilization [*Marin-Spiotta et al.*, 2011; *Sollins et al.*, 2009]. Factors influencing soil storage in both soil organic matter (SOM) and DOC at the global scale include temperature [*Prior et al.*, 2005; *Post and Kwon*, 2000; *Wynn et al.*, 2006], forest community [*Guo and Gifford*, 2002], mineralogy [*Six et al.*, 2000, 2003, 2004], and available moisture [*Kalbitz and Kaiser*, 2003; *Marschner and Kalbitz*, 2003; *Prior et al.*, 2005]. However, little is known about the extent to which these factors influence spatial patterns in SOM and DOC at a significantly smaller, "watershed scale" ($< 1\,\mathrm{km}^2$), particularly in complex terrain, and whether or not they are recognizably affected by forest history and stand development. In this study, the relationships between aboveground structure and function, specifically aboveground net primary productivity (ANPP) and stand composition, and soil C dynamics were explored, specifically whether or not SOM and DOC are related to ANPP, litter fall, and N mineralization. Recent analyses have suggested that processes governing soil C may display emergent "hot spot" or "hot moment" patterns; that is, specific locations or times C is unexpectedly augmented due to a synergistic intersection of ecosystem patterns and processes [*Creed et al.*, 2002].

Additional supporting information may be found in the online version of this article.

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For DOC, these hot spots and moments often correspond to belowground flow paths influenced by certain topographic conditions (hot spots) during certain developmental stages (hot moments) of the forest; for SOM, hot spots and hot moments indicate where and when soil C is preferentially stored in either the relatively labile, partially decomposed organic matter (light fraction or LFC, in the sense of *Sollins et al.* [2006]) or else in more stable forms, associated and protected by mineral matter (heavy fraction or HFC). Our study assesses both the possibility of relationships between stand structural features (e.g., ANPP, biomass) and ecosystem function [*Acker et al.*, 2002] being emergent properties or functions of fixed topographic and biological gradients. Our objective is to quantify how topography and stand composition (1) integrate with one another and (2) affect belowground C stocks and losses. To determine this, we compared various belowground soil C stores and DOC with several measurements of aboveground ecosystem productivity over a number of sites measured during a 2 year period in complex terrain.

[3] ANPP has been correlated with litter fall, which is an important short-term contributor to SOM and DOC [*Gentile et al.*, 2011; *Heal et al.*, 1997; *Hongve et al.*, 2000; *Paustian et al.*, 1997a, 1997b; *Rasse et al.*, 2005]. Both SOM and DOC should also be related to environmental conditions that influence ANPP. In complex mountainous terrain, factors such as soil depth, soil rockiness, and solar insolation have been shown to influence SOM [*Moore et al.*, 1993; *Post and Kwon*, 2000]. These environmental factors affect stand composition and ANPP, specifically the quality and quantity of litter fall and rates of decomposition, thus influencing stores and stability of SOM, DOC production, N mineralization, and DOC export [*Adrianarisoa et al.*, 2010; *Cole*, 1982; *Kalbitz and Wennrich*, 1998]. However, several factors can alter the relationship between litter production and SOM content. The quality of litter, specifically N content and the biochemistry of organic C, can alter the proportion of litter C that is respired versus stored; thus, the amount of litter that becomes SOM can vary with forest community composition [*Berg and Meetenmeyer*, 2002; *Trofymow et al.*, 1995]. Similarly, SOM stability is influenced by soil properties, such as physical protection and mineral association, and in turn affects other processes such as microbial respiration and DOC leaching [*Six et al.*, 2002, 2003, 2004]. Different pools of SOM may also respond differently to changes in plant production and environmental variables. Because light fraction (LFC) is relatively ephemeral, it should respond quickly to changes in productivity and litter fall. While HFC is also related to biotic factors, it has been shown to have important relationships to soil mineralogy as well [*Hongve et al.*, 2000; *Qualls et al.*, 1991; *Sollins et al.*, 2006] and may be more responsive to soil microclimate. However, studies documenting SOM storage and stability have largely been limited to experimental manipulations of controlled sites using cropping and tillage rather than the natural variability in complex terrain [*Beare et al.*, 1994; *Biederbeck et al.*, 1994; *Bremer et al.*, 1994]. Microclimate and water availability to decomposers, as well as the potential for litter and soil erosion, could also obscure any direct relationship between litter production and SOM stores and can be expected to be related to topography and soil characters such as rock content across a complex landscape.

[4] In complex mountainous terrain, specifically a small, previously clear-cut watershed in the western Cascades range of Oregon, we explored the relationships between biomass, ANPP, stand structure, litter production, SOM pools, N mineralization, and DOC content and export, and how these relationships are affected by complex terrain. We hypothesized that ANPP would be positively related to litter fall and to labile (light fraction) C, but that stable (heavy fraction) C and DOC would be also affected by soil and topographic features such as slope, soil rock content, and exposure. Both DOC and heavy fraction C are directly related to topography; DOC travels along topographically determined flow paths and HFC relies on soil mineralogy often associated with distinct topographic features. In these (DOC, HFC) belowground pools particularly, relationships between current productivity measurements and landscape indices might be obscured or seasonally emergent. We also hypothesized that stand structure, particularly hardwood versus coniferous biomass, could alter the relationships between productivity and belowground C stores and that stand composition might be the driver for emergent properties, if extant on this site. For example, the greater mass of leaf litter from drought-tolerant hardwoods on warmer, drier sites could result in more light fraction C, N mineralization, and DOC export. As the soil in young forests is not C saturated, we expected that % C in the heavy fraction would be positively correlated with ANPP and litter fall, which corresponds to the notion that both biological and topographical factors should influence soil C storage in the heavy fraction (in the sense of *Six et al.* [2004]).

2. Site Description

2.1. Vegetation and Harvest

[5] Watershed 1 (WS1) is a 96 ha catchment on the H.J. Andrews Experimental Forest in the western Cascades Range in Oregon. Originally part of a "paired watershed" experiment to understand the effects of forest harvest on stream flow dynamics, WS1 was clear-cut from its original condition of 450 year old *Pseudotsuga menziesii* (1962–1966), burned (1967), and replanted (1968–1971) with *Pseudotsuga menziesii* seed and seedlings [*Halpern and Franklin*, 1989; *Halpern and Franklin*, 1990]. The harvest of WS1 was conducted using a small area of skidder-based logging (near the landing at the stream outlet) and a large extent of skyline logging. Due to the immense size of the individual trees and the instability of the slopes, the logging progressed slowly over 4 years and seven spatially distinct harvest units as new technology were implemented, and it has been documented that early regeneration, particularly of shrub trees *Acer circinatum* and *Rhododendron maximum*, had established on some of the early harvested units prior to whole-landscape burning in 1967. Burning was "hot and satisfactory" and large stems not removed in logging but downed by burning were removed from the lower one third of the watershed to clear the stream pathway. Four attempts at regeneration were made; the first attempt was an aerial reseeding over the whole landscape; the second through fourth were manual replanting on the south facing slope, with maximum planting attempts devoted to an "unplantable" area in harvest documentation. The plantings in such areas were ultimately not successful in generating as much biomass as other parts of the site.

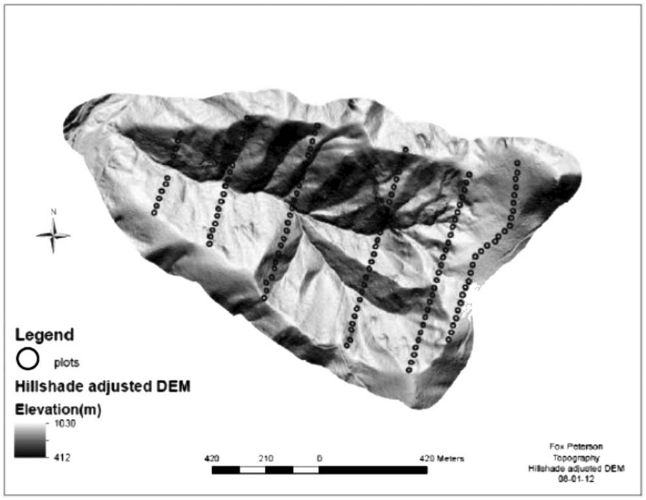

Figure 1. Sampling schematics on watershed 1; 132 plots on six transects perpendicular to stream.

[6] The current site vegetation is dominated by 55 year old, 20 to 30 m height cohort of *Pseudotsuga menziesii*, most of which was developed from planted seedlings. However, other species such as *Tsuga heterophylla*, *Alnus rubra*, *Thuja plicata*, *Castanopsis chrysophylla*, *Acer macrophyllum*, and *Prunus emarginata* have naturally seeded in from nearby old growth stands and alder-dominated riparian areas. *Acer circinatum* and *Rhododendron macrophyllum* exist as tall shrubs. Ground vegetation is primarily *Polystichium munitum*, *Gaultheria shallon*, and *Mahonia aquifolium*, all of which have been present on the stand since establishment.

2.2. Climate and Topography

[7] Mean annual precipitation on site is approximately 2300 mm with a mean temperature of 2°C in January and 18°C in August, with a 2°–6° average daily range, as is typical of the region. WS1 is near the confluence of Lookout Creek with the McKenzie River, at a relatively low elevation (410–1080 m). Parent material is largely andesite and breccia, with both green and red breccias present, as well as blackish andesitic scree and large, potentially glacially deposited boulders [*Swanson and Jones*, 2002]. Four series of andisols exist on the site: Frissell, Budworm, Limberlost, and Andesite Colluvium, as well as a distinct "rock" area [*Rothacher et al*., 1967; *Dyrness*, 1969]. Topography controls the microclimate, which differs distinctly by north and south facing aspects, particularly with respect to insolation. Diurnal fluctuations in temperature due to adiabatic cooling on steep slopes yield nocturnal cold air drainages on approximately 80% of summer nights [*Pypker et al*., 2007]. Nutrient concentrations of WS1 have not been studied in depth, but it has been shown that the site is limited primarily by N, which is typical of the region as a whole [*Vitousek and Howarth*, 1991].

3. Methods

3.1. Vegetation (Sampling, Biomass, and ANPP)

[8] Long-term data for the site were available in the form of forest inventory flat files consisting of diameter at breast height (DBH) measurements for each individual tree on 131 circular plots with an 8.92 m radius (Figure 1). These plots are arrayed systematically along six transect lines which bisect WS1 perpendicular to a "y-shaped" tributary and span the 1 km^2 site at an angle of approximately 220°SSW to 40°NNE *Lutz*, [2005]. DBH was measured on all trees greater than 1 cm; diameter at base was used as a proxy for all trees less than 1 cm, and conversion equations were calculated by *Lutz* [2005]. From DBH, to determine the biomass of individual trees, allometric equations in the Pacific Northwest Biomass Component Equation Library [*Halpern and Means*, 2011] were applied to the appropriate species following the precedent set in *Lutz* [2005] and *Lutz and Halpern* [2006]. Because the plots were initially laid out on the surface rather than aerially, we calculated plot area using an elliptical adjustment based on gradient and from this determined biomass per unit area (Mg/ha). We calculated ANPP based on the *Acker et al*. [2002] method, also precedent in *Lutz* [2005] and *Lutz and Halpern* [2006]. This method does not directly incorporate litter fall data. We mapped the aboveground biomass and ANPP for the 131 remeasurement plots and used spherical kriging to extrapolate across the spatial extent (ArcGIS 9.3.1, "Geostatistical Analyst" Toolkit, Environmental Systems Research Institute (ESRI) 2009).

3.2. Soil Sampling

[9] During the summer of 2011, soil cores were taken from all accessible vegetation plots (124 of 133 plots) using an Oakfield soil corer. Eight cores were taken at random locations within the plot, with the intent of capturing microtopographic and microclimatic variability. Soil cores did not include the O horizon and were 10 cm long and 1.7 cm in diameter, unless soil thickness was less than this amount, in which case soil cores reflected the maximum possible penetration up to 10 cm. Sixteen plots selected to represent the variability in biomass across the watershed based on 2007 lidar analyses were cored subsequently in March of 2012 for the purpose of obtaining measurements of soil moisture. These 16 plots also house the lysimeters and litter traps used to measure mobile soil water and litter fall, respectively. Not all plots cores samples generated enough material for reliable density fractionation.

3.3. Lysimeter Collections

[10] In summer of 2010, we installed two Prenart Super Quartz lysimeters at 70 cm depth and at a 53° angle to the soil surface on the 16 intensively measured plots, surrounding them by silica flour to facilitate contact with the soil and protecting them with polyvinyl chloride housing. Lysimeter leachate was collected during the rainy seasons (October through May) between 2010 and 2012. Lysimeters were primed to 103.41 kPa after each collection and usually collected 2 days following priming. During the 2010–2011 season, 10 lysimeter collections were attempted, with between two and five lysimeters yielding water on any given run. During the 2011–2012 season, four lysimeter collections were made, with five to seven lysimeters yielding water on any given run. Climactic variability occurred between the 2 years. The rainy season of 2010–2011 began earlier (October) than that of 2011–2012 (November) and did not extend as late into the spring (April versus May).

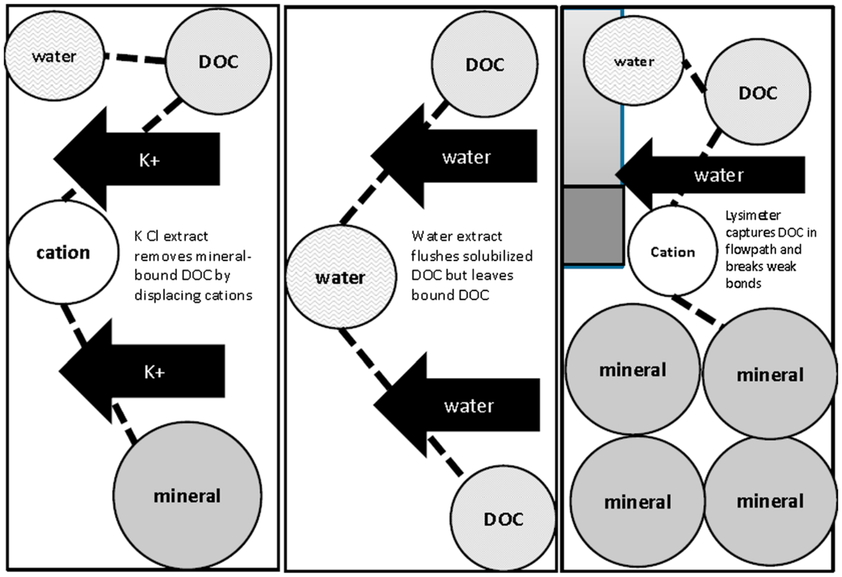

Figure 2. Extraction methods and soil pools: (left) KCl extraction, (middle) water extraction, and (right) tension lysimeters.

Additionally, during the 2011–2012 season, cooler temperatures and a lower snowline prevented access to some of the high-elevation lysimeters during the early season. We averaged both lysimeters on each plot across time and with one another in order to determine a value for each plot. Because this method has high variability, we use the other methods of measuring soil water (KCl and water extraction) to validate or further explore patterns observed in DOC.

3.4. Soil Depth

[11] We visited all of the accessible long-term remeasurement plots during the spring of 2011. Soil depth was measured using the knocking pole method. This period was selected because of the soil penetrability afforded by moist conditions. The knocking pole was penetrated into the soil perpendicular to the surface to a maximum depth of 120 cm to account for 90–95% of roots [*Coutts et al.*, 1999; *Gasson and Cutler*, 1990; *Gilman*, 1990]. The six measurements taken were averaged to a plot-scale mean that was used to estimate actual soil depth.

3.5. Soil Rock Content

[12] Soil rockiness (percent by volume) was measured from excavations of 16 sets of two soil pits with a 600 cm^3 volume on the same subset of plots. In one of these pits, lysimeters were later placed. Soils were removed from the site manually and returned to the laboratory where they were separated by depth (0–10 and 10–20 cm) and sieved by particle size (< 2, 2–5, and > 5 mm). Rock bulk density was calculated using the submersion method for each plot individually because volcanic rocks are often lighter than the traditional 2.65 g/cm^3 value. Soil rockiness was computed on a volume-of-rock to volume-of-soil basis facilitated by the individual density calculations. We developed a metric of effective soil depth (ESD) similar to that which is used in agriculture to imply the soil volume available for moisture storage [*Wolf and Van Diepen*, 1995; *Verseghy*, 2007]. ESD was calculated as

$$\text{Total Depth(cm)–Percent Rockiness} \times \text{Total Depth(cm)} = \text{ESD(cm)} \tag{1}$$

[13] The ESD metric was our primary metric for quantifying potential belowground moisture holding capacity.

3.6. Litter Fall Collections

[14] We collected litter from 16 of the long-term plots on WS1. These plots were selected to represent the distribution of biomass on the watershed based on an imputed measurement of percent cover and tree height determined in lidar reconnaissance in 2008. Litter collections (from square ground

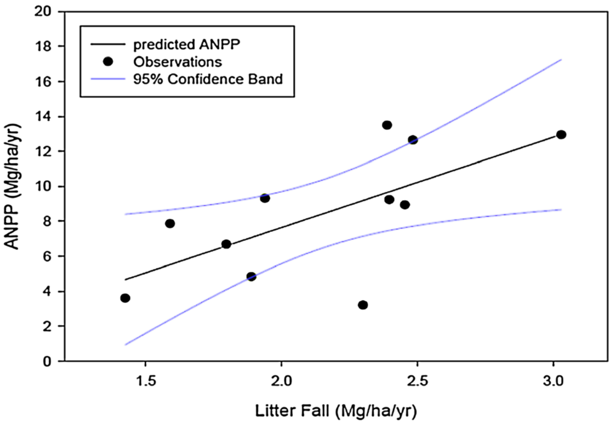

Figure 3. Litter fall (Mg/ha/yr) averages by plot for 2010–2012 versus ANPP for the most recent remeasurement interval of 2001–2007. ($R^2 = 0.65$). Correlations between ANPP and N mineralization and N mineralization and litter fall were poor and are therefore not displayed.

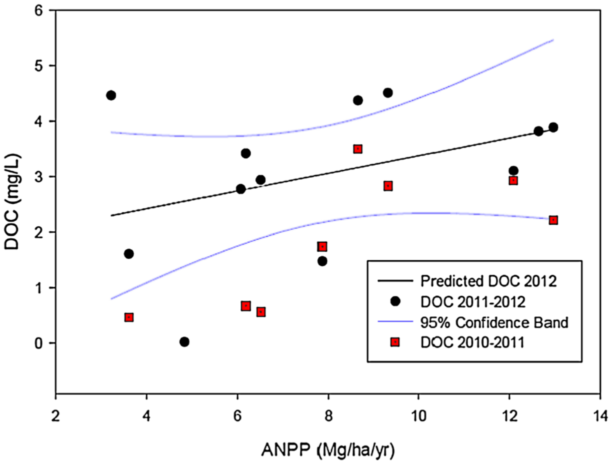

Figure 4. Lysimeter (mg/L) collected in 2010–2011 and 2010–2012 versus current ANPP. Lysimeter-extracted DOC from 2011 to 2012 was well correlated with ANPP ($R^2 = 0.52$). Lysimeter-extracted DOC from 2010 to 2011 was not correlated ($R^2 = 0.30$).

traps of 0.1849 m^2 with mesh linings) were conducted seasonally for the years 2009–2011, from August to August in each year. Trap status and any anomalies in trap content (bark, debris, etc.) were recorded. Fine and coarse litter were brought back to the lab and separated with a 30.48 cm hardware cloth with 12.5 cm openings. Sieving was conducted using a cloth screen small pieces passed through the screen, and after the separation, twigs that slipped through the screen were returned to the coarse fraction. After the separation, wet weight was recorded, then the sample was oven-dried (at 30°C) until a stable weight was reached which was determined to be the dry weight. Three traps were damaged between collections due to local wind events resulting in trap turnover and branchfall, so litter mass accumulated for these plots was only recorded prior to damage and a note was taken on the number and extent of damage.

[15] To calculate dry mass of leaves (in Mg) per hectare per period (length of the remeasurement interval), three conversion factors were used to account for the set of plots on which only three or four samples were valid due to the damage:

$$\text{Litter fall rate}(\text{Mg/ha yr}^{-1}) = 0.1849\ \text{m}^2 \times \text{Number of Traps} \times \text{Dried Mass of Leaves}(\text{g}) \times 10^{-8} \times \text{conversion factor} \quad (2)$$

[16] For the first year, leaf collections were precise to 365 days for almost all plots. Thus, the sum of the collected masses per hectare over the course of that year represented the annual collection. When plots were collected on subsequent days, extending the annual length, one additional day was included in the annual collection period, and the influence of that period on the sum was weighted by a conversion factor of 0.9696. When a trap was damaged, mean values from the other collection periods (early summer and winter) were weighted to the appropriate amount of days and used as a proxy for the missing measurements. When extremely coarse materials such as large chunks of bark and rotted log were found in the sample during one remeasurement, the data were not removed from the set, however, the anomaly was noted. We recognize that belowground inputs may also contribute to soil C; however, it has been shown on the Detritus Input and Removal Plots (DIRT) proximal to our site that 90% of soil C and export in this ecosystem are the result of aboveground inputs [*Lajtha et al.*, 2005]. Therefore, these inputs were not included in this analysis.

3.7. Topography

[17] We developed a set of 12 topographic metrics within ArcGIS 9.3.1 (ESRI, 2009) using a digital elevation model (DEM, 10 m resolution) and a lidar bare Earth map (1 m resolution, reconnaissance flown in 2008). Lidar was flown with a minimum of nine returns per m^2 to approximate vertical protrusions within 13 cm accuracy and horizontal cover within 1 m accuracy. For 1 m topography, the final returns for each of the voxels were averaged to determine bare Earth altitude [*Lefsky et al.*, 1999]. To address the influence of topography on stand structure, we derived metrics from the DEM or lidar bare Earth map using ArcGIS's "Spatial Analyst toolkit" or the downloadable "Topography toolkit" (available from ESRI, 2010). We specifically assessed the

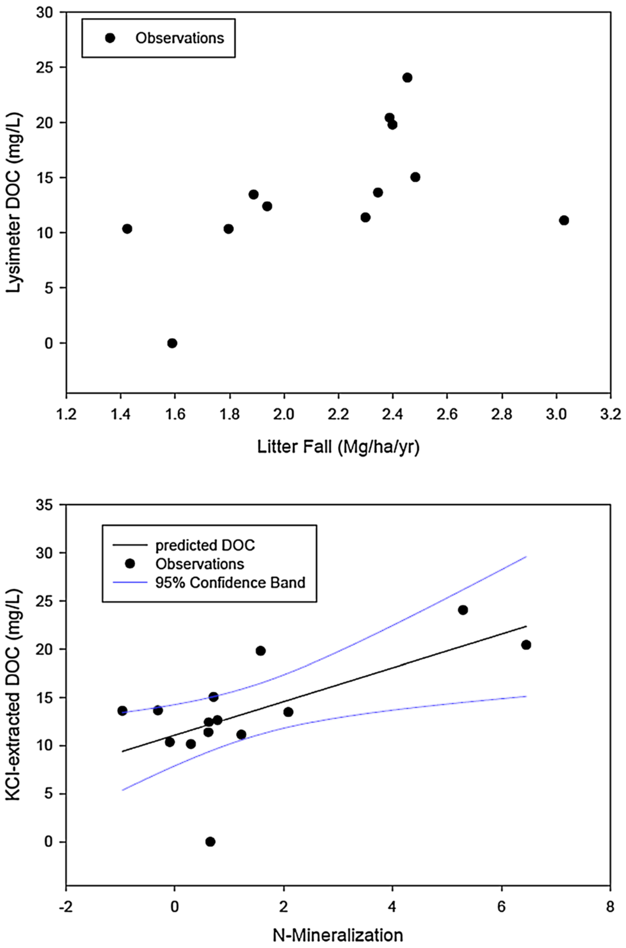

Figure 5. KCl-extracted DOC (mg/L) versus litter fall from 2010 to 2012 ($R^2 = 0.26$) at the whole watershed extent; KCl-extracted DOC versus N mineralization from a 1 month incubation in 2011 ($R^2 = 0.41$). N mineralization strongly influenced by outlier plots.

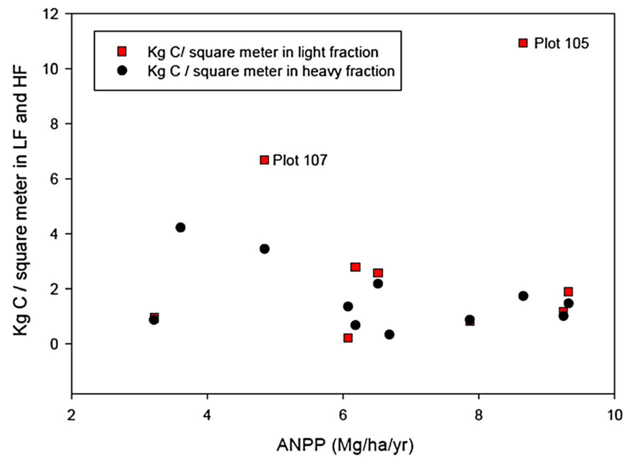

Figure 6. Poor correlation between light fraction C (kg C/m^2) and ANPP as calculated from the 2001–2007 remeasurement interval; mild correlation between heavy fraction C (kg C/m^2) and ANPP as calculated from the 2001–2007 remeasurement interval ($R^2 = 0.18$).

topographic metrics of aspect (compass degrees of the slope ranging from 0 to 360), slope (degrees, ranging from 0 to 65 on this site), elevation (meters, from 485 to 1080), maximum solar insolation (watts per square meter, calculated using topographic shape and ray-tracing algorithms in ArcGIS 9.3.1), upslope contributing area (calculated using the D8 model defined in *O'Callaghan and Mark* [1984]), angle to the horizon, Beer's Index (an index of potential heat, calculated in ARCGIS9.3.1.), wind exposure, topographic wetness index (defined as the natural log of the contributing area divided by the slope angle), and Jenning's landform classifications [*Rothacher et al.*, 1967; *Rothacher et al.*, 1967; *Swanson and Jones*, 2002]. These topographic metrics we selected serve as remotely sensed proxies for belowground resource distributions or ecosystem forces that could affect them.

3.8. Nitrogen Mineralization

[18] Measurements of N mineralization potentials were conducted following the protocols in the Long-Term Ecological Research Soil Methods handbook [*Robertson et al.*, 1999].

[19] From each plot, one 25 g soil aliquot was incubated for 28 days at 60% moisture capacity in a dark chamber. Samples were extracted with 100 mL of 1 *M* KCl and filtered through glass filters. A second set of samples from each plot was immediately extracted following return from the field. The NH_4-N and NO_3-N contents of each sample were assessed using a Lachat Autoanalyzer. During the autoanalysis period, extractions were preserved at 4°C while not being used in the machine. We expressed N mineralization in two ways: (1) in terms of the N mineralization of soil (mg/g soil) and (2) on an areal basis corrected for rock content and large roots (Kg/m^2).

3.9. Density Fractionation

[20] An increasingly common technique to separate soil C into functionally meaningful pools is density fractionation which partitions soil C based on density into "light" and "heavy" fractions [*Buyanovsky et al.*, 1994; *Cambardella and Elliot*, 1992; *Christensen*, 1992, 1996; *Oades*, 1993; *Six et al.*, 2004]. The light fraction (LFC), which has a density of less than 1.85 g/cm^3, is based on the density of litter (1.65 g/cm^3) plus mineral contamination. The heavy fraction (HFC) reflects the load that often forms on primary and secondary minerals. From each of the plot samples collected and air-dried, two 25 g subsamples were used for density fractionation (two replicates per plot). Organic materials greater than 2000 μm were removed. Subsamples were mixed and shaken with sodium polytungstate solution with a density of 1.85 g/cm^3 for 2 h and centrifuged for 20 min (following *Sollins et al.* [2006]). Light fraction was aspirated following centrifuging. Heavy fraction remaining in the centrifuge tubes was then washed using distilled and deionized (DDI) water. Dried soils were then ground and analyzed for C in a Leco TrueSpec Micro. We expressed the light and heavy fractions of C in three ways: (1) C density, the % C in the heavy fraction; (2) the C content of the soil (mg C/g soil); and (3) the C content on an areal basis in terms of Kg C/m^2 soil to a depth of 30 cm, which was corrected for rock content and large roots using % C data in conjunction with the calculation of effective soil depth. This created a spatially relevant measurement of C that included limitations due to rockiness.

3.10. DOC Analysis

[21] Concentrations of DOC were measured with a Leco Micro Spec on 25 g subsamples. We measured three distinct DOC pools. (1) "KCl-extractable" DOC was determined from an extraction with 1 *M* KCl and represents all DOC including that bound to minerals by cation bridges. Biologically available C is separated from soil using a salt-based extraction (KCl extraction), which should capture the most potentially available C because cation bridges binding DOC to soil minerals are displaced by the salt's cations [*Jones et al.*, 2012; *Zsolnay and Steinweg*, 2000; *Zsolnay*, 2003]. (2) "Water-extractable DOC" (WEDOC) was determined using DDI water and represents soluble DOC not

Table 1. Summary of Linear Correlation Coefficients (R^2) Between Four Topographic Factors (Elevation, Slope, Beer's Heat Index (Beer's Index)), and Topographic Position Index (Topographic Position) and kg C/m^2 in the Light Fraction and Heavy Fraction by Soil Type[a]

	Elevation	Slope	Beer's Index	Topographic Position	Sample Size
All soils (mg C/m^3)					96
Heavy fraction	0.43	0.05	0.4	0.04	
Light fraction	0.22	0.09	0.86	0.62	
Frissell soil					53
Heavy fraction	0.41	0.38	0.09	0.02	
Light fraction	0.83	0.61	0.12	0.73	
Limberlost soil					21
Heavy fraction	0.39	0.68	0.88	0.17	
Light fraction	0.2	0.15	0.58	0.09	
Budworm soil					8
Heavy fraction	0.79	0.03	0.08	0.86	
Light fraction	0.01	0.61	0.05	0.01	
Andesite colluvium soil					13
Heavy fraction	0.34	0.17	0.06	0.46	
Light fraction	0.01	0.23	0.95	0.95	

[a]Standard deviation amid the light fraction was 4.38 kg C/m^2 and amid the heavy fraction was 2.11 kg C/m^2.

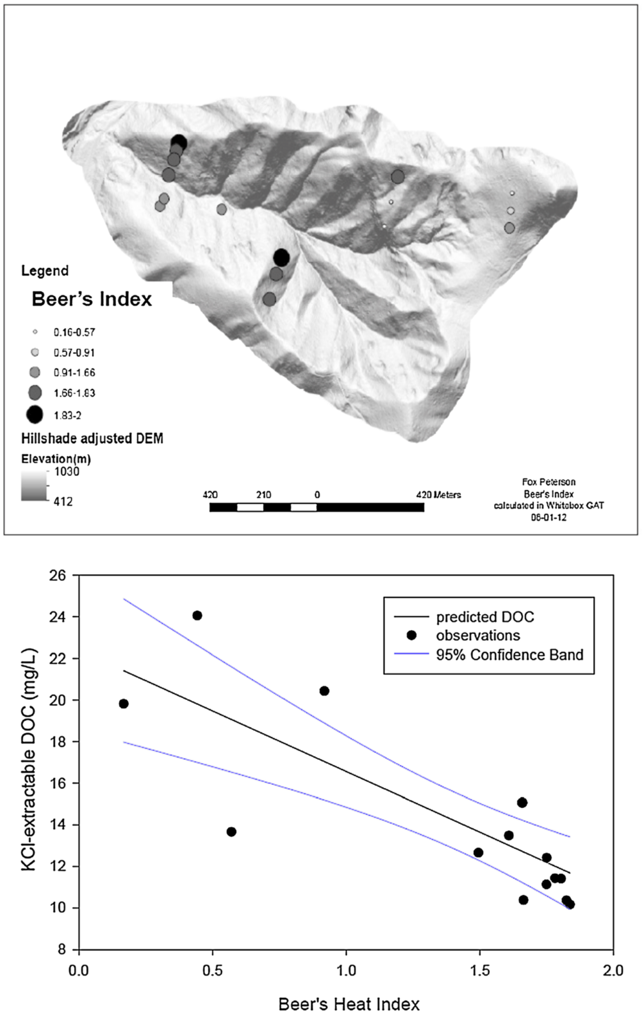

Figure 7. Map of Beer's Heat Index on WS1; KCl-extracted DOC (mg/L) versus Beer's Heat Index. Low values of Beer's Heat index indicate protected, cool locations and high values indicate exposed, hot locations.

limited to the saturated flow path. Water extractions physically separate soluble DOC from the soil but do not displace mineral bonds. (3) "Lysimeter-collected DOC" was the collected leachate from the tension lysimeters. Tension lysimeters capture leachate in the soil and also draw off some bound DOC (pressure gradients) from soil surfaces, but are contingent on soil saturation and therefore adequate precipitation events (Figure 2).

3.11. Statistical Analyses

[22] Linear and multilinear models were fit in MATLAB (MathWorks, 2010) using the "polyfit" and "stepwise" tools. We only display the R^2 values of the fits here when the P values of the selected parameters are significant ($P < 0.001$) or, in select cases, as examples of lack of correlation. Linear fits in the figures are depicted using Microsoft Excel 2010. When a nonlinear fit was tested, the "nlmefit" tool in MatLab was used; however, none of our results indicated that nonlinear models were more useful than linear models for predicting soil C. Additionally on this site, a random forests analysis was conducted to determine the relationships between productivity and belowground correlates, and it was determined that soil characteristics were the strongest predictors for aboveground productivity when expressed as generalized "soil types."

3.12. Data Management

[23] Long-term data from the H.J. Andrews Experimental Forest were used for this study and are available online at http://andrewsforest.oregonstate.edu under the "data" tab. Data collected on the intensively sampled plots are included as supporting information to this text.

4. Results

4.1. Correlations Between ANPP and Litter Fall, N Mineralization, and DOC

4.1.1. Descriptive Statistics Regarding ANPP, N Minerali-zation, and DOC

[24] The mean ANPP, calculated from the 2001–2007 remeasurement interval, on WS1 is 7.54 ± 3.46 Mg/ha/yr for all 132 plots. The mean N mineralization on reliably sampled and analyzed plots (108 of 132 total plots) is 0.187 ± 2.11 (μg N/g soil/d) and this measurement is based on soils collected in 2011. The mean litter fall as determined as an average of data across all seasons collected between 2010 and 2012 is 2.32 ± 0.90 Mg/ha/yr.

4.1.2. Correlations Between ANPP, N Mineralization, and DOC

[25] ANPP (hereafter called "current ANPP," calculated from the 2001–2007 remeasurement interval following the methods of *Acker et al.* [2002]), was positively correlated with litter fall ($R^2 = 0.65$), but not N mineralization ($R^2 = 0.12$), and N mineralization was not correlated with litter fall ($R^2 = 0.05$) (Figure 3). ANPP was also positively correlated with lysimeter-collected DOC during both years of collection with the second year of analysis (2011–2012) best correlated to current ANPP ($R^2 = 0.54$) (Figure 4). Exponential regression slightly increased the correlation

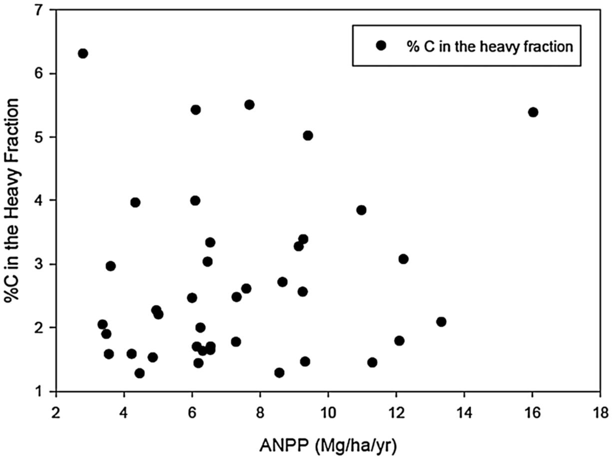

Figure 8. Percent C in the heavy fraction calculated from samples taken in 2011 versus ANPP for the current remeasurement interval (2001–2007) shows no correlation ($R^2 = 0.04$). Classifying WS1 by species groups or aspects did not improve the correlation.

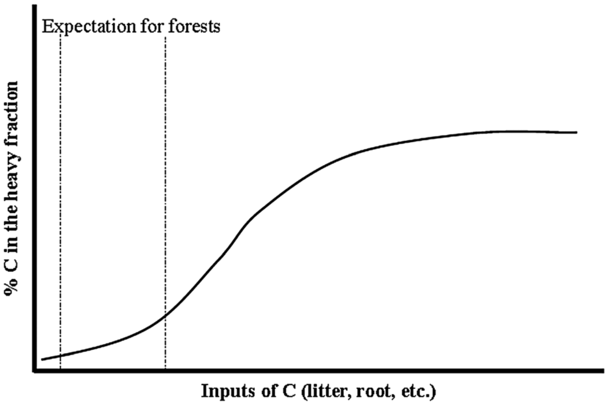

Figure 9. The expectation was that a positive “linear” relationship between C inputs (litter or ANPP) and kg C/m^2 in the light and heavy fractions, as well as % C in the heavy fraction (diagrammed) would exist because this forest is not yet near the point of C saturation. However, we found no correlations between any of these.

(transformed $R^2 = 0.64$), but this is likely due to reduction in variance from the transform, not to an actual physical phenomenon. KCl- extracted DOC ($R^2 = 0.17$) and WEDOC ($R^2 = 0.01$) were not correlated with ANPP.

4.2. Weak Correlations Between Litter Fall and N Mineralization and DOC: Driven by Outliers

4.2.1. Descriptive Statistics Regarding DOC in Three Pools

[26] KCl-extracted DOC from 2011 soils had a mean value of 13.128 ± 5.17 (mg/L), WEDOC had a mean value of 5.01 ± 2.29 (mg/L), and DOC collected from lysimeter leachate from years 2010 to 2012 had a mean value of 3.033 ± 1.33 (mg/L). Maximum values for KCl-extracted DOC, WEDOC, and lysimeter DOC were 24.06 (ANPP on this plot is 13.499 Mg/ha/yr; litter fall is 3.028), 4.52, and 11.98 mg/L, respectively (from the same plot, ANPP on this plot is 9.321 Mg/ha/yr and litter fall is 1.938).

4.2.2. Correlations Between Litter Fall, N Minerali-zation, and DOC

[27] Neither litter fall nor N mineralization was correlated with any measure of DOC. The best relationships found were between KCl-extracted DOC and litter fall ($R^2 = 0.26$) and available DOC and N mineralization ($R^2 = 0.41$ for N mineralization per g soil); however, this correlation was strongly influenced by outlier plots (Figure 5). For example, on one plot with a very low available DOC (0.56 mg/L), recent suppression and windthrow have caused substantial mortality and declining productivity. The two plots with very high (> 20 mg/L) KCl-extracted DOC are located in a moist area near the stream outlet. These plots have large upslope contributing areas; therefore, they serve as pour points for much of the watershed.

4.3. No Correlations Between ANPP, Litter Fall, N Mineralization, and SOM

[28] ANPP was not correlated with light fraction C (LFC) ($R^2 = 0.01$) or heavy fraction C (HFC) ($R^2 = 0.18$) expressed on an areal basis. Also, litter fall and N mineralization were not correlated with LFC or HFC expressed on an areal basis (Figure 6). Two outlier plots with exceptionally high LFC were located near the stream outlet (plots 105 and 107). These plots are also in the same moist area plots as those with very high values of KCl-extractable DOC. These moist plots have many *Alnus rubra* present and are saturated throughout much of the year due to hillslope position. Percent C in the heavy fraction was not correlated with ANPP ($R^2 = 0.04$), N mineralization ($R^2 = 0.01$), or litter fall ($R^2 = 0.17$) (Figure 6).

4.4. Topography Indicative of Elevated ANPP, Litter Fall, SOM, and DOC

[29] On warmer, drier sites, ANPP is inversely related to LFC and DOC. Warmer, drier sites are found on this watershed at (a) high elevations with (b) steep slopes and (c) an exposed surface (a convex topographic position), the combination of which may be represented by an elevated value of the (d) Beer’s Heat Index (Beer’s Aspect), which represents the potential heat to any location on a watershed based on surface shape and radiation angles [*Stage and Salas*, 2007; *Pypker et al.*, 2007]. LFC content (mg C/g soil) correlated with the Beer’s Heat Index variable over the whole watershed as well as within soil type divisions (Table 1). Although it appears that there is a particularly strong correlation between the Beer’s Index on the andesite colluvium soil type and LFC content ($R^2 = 0.95$), the sample size was small ($n = 13$). LFC content on all soil types versus Beer’s Index showed a strong positive linear trend ($R^2 = 0.86$) when measured across all samples ($n = 96$). HFC content (mg C/g soil) correlated with elevation ($R^2 = 0.43$). When classified by soil types, HFC content correlates positively with slope on Budworm soils ($R^2 = 0.43$) but negatively with slope in the Limberlost soil type ($R^2 = 0.68$) and Frissell soil type ($R^2 = 0.38$).

[30] Beer’s Heat Index was also moderately correlated with KCl-extracted DOC ($R^2 = 0.52$) (Figure 7). This correlation was slightly improved when the watershed was classified by aspect (isolating data from only the south facing aspect, $R^2 = 0.78$, or the north facing aspect, $R^2 = 0.62$). However, the correlations were largely influenced by outlier plots located on the ridgeline and in the “wetland” area.

4.5. Heavy Fraction Saturation: Not Related to ANPP

[31] We found no relationship between % C in the heavy fraction and ANPP. There was also no correlation between % C in the heavy fraction and ANPP when the site was classified by aspect, or divided into groups dominated by conifers and hardwoods (Figure 8). Figure 8 displays only the lack of correlation at the whole watershed extent.

4.6. Soil Rock Content Indicates Threshold Behavior in Aboveground and Belowground C Stores

[32] ANPP, DOC, SOM, and litter fall were not correlated with soil rock content. However, we did find that there was a drastic decline in soil C, ANPP, and litter fall above soil rock contents of approximately 30%.

5. Discussion

5.1. ANPP Related to Litter Fall and DOC, Not SOM

[33] In a complex terrain, we expected that ANPP would be positively correlated with litter fall because production and turnover of foliage should be related to production of biomass as a whole. Foliar biomass is determined from total aboveground biomass, so an increase in ANPP (as calculated

as a difference in biomasses) should lead directly to an increase in litter fall. Our ANPP calculations were based entirely on change in biomass over the interval and did not include litter fall explicitly, which avoids potential issues with statistical independence. Because aboveground litter fall is a primary source of C to soil, we predicted that the C content in both the labile and stable SOM would be positively correlated with both litter fall and ANPP, although these relationships might vary over space and time, and could be substantially altered by environmental factors such as soil depth or rock content. Specifically, we expected litter fall, and ANPP, to be tightly correlated with LFC in particular, as LFC is simply modified and slightly altered litter debris. However, we did not find any relationship between LFC and either litter fall or ANPP.

5.2. Priming as a Potential Mechanism for Explaining SOM Distribution and Losses

[34] One explanation for these results may be that priming of soil organic C by litter could actually cause increased respiration of SOM [*Kuzyakov*, 2010]. Priming is the stimulation of soil organic carbon (SOC) turnover in the presence of increased inputs (such as litter fall or woody debris). Results from the nearby DIRT site [*Lajtha et al.*, 2005] have shown that while experimentally increased woody debris inputs have led to increased levels of LFC, increased needle inputs have led to increased respiration, resulting in trends toward lowered LFC with increases in labile litter additions [*Sulzman et al.*, 2005, *Crow et al.*, 2009]. This priming effect may not last for more than a decadal timescale; results from a 50 year DIRT experiment have shown increases in LFC with long-term increases in litter inputs. Because our forest is about 65 years old, we expected to see results more like these, rather than to see the effects of priming. However, priming also may be very site dependent; litter addition experiments in a dry forest in Hungary resulted in immediate increases in soil C [I. Fekete et al., The effects of detrital inputs on soil carbon content and CO_2 release in a Central-European deciduous forest, Forest Ecology and Management, in review, 2013], possibly due to site conditions less conducive to litter and SOM decomposition. Clearly, the relationship between litter production and soil C accumulation is complex and not well understood.

5.3. Litter Fall: Not Related to SOM

[35] We also expected litter fall to be correlated with C density (% C of the heavy fraction–g C/g heavy fraction), as we expected that soils in this forest would be undersaturated [*Huggins and Fuchs*, 1997; *Huggins et al.*, 1998; *Paustian et al.*, 1997a, 1997b; *Reicosky et al.*, 2002; *Six et al.*, 2002; *Stewart et al.*, 2007, 2008, 2009] with respect to mineral-protected organic matter. For example, *Paustian et al.*, 1997a, 1997b found that soil C increases without limit with increases in C inputs while *Six et al.* [2002] and others studying agricultural ecosystems—largely those dominated by *Zea mays*—suggested that soil C should increase following a saturation curve, although with the HFC saturation capacity lower than the LFC. Our analysis purposefully focused on aboveground inputs exclusively because previous analyses on the same site [*Lajtha et al.*, 2005] have indicated that belowground inputs are not significant sources of C to the belowground pool in this ecosystem. We had expected to find an increase in C density with increasing aboveground C inputs because young forests may still have low C inputs overall and represent the beginning of a saturation curve (Figure 9). That we did not find this suggests that (a) soil respiration, and destabilization of either LFC and/or HFC, increases with increases in litter fall due to priming, (b) the forest has already reached C saturation, (c) not enough time has elapsed for there to be measurable increases in HFC in sites with high productivity, or (d) that other variables, either biotic or abiotic, confound the relationship between litter fall inputs and C density in the mineral fraction of soils. We think it unlikely that the forest mineral soil has reached saturation, although there is no evidence one way or the other. Priming of HFC by litter is quite possible, and priming of LFC would lead to lower amounts of C that could be transferred to mineral soil. Finally, it is also quite possible that variations in site characteristics, such as water availability or heat loading, could cause enough variation in rates of litter decay and/or soil respiration to obscure any relationship between litter inputs and soil C accumulation. Indeed, the fact that Beer's Heat Index is highly variable even across this small area emphasizes the heterogeneity in microclimate that exists on complex terrain.

5.4. Litter Fall Not Related to N Mineralization

[36] We also expected litter fall to be positively correlated with N mineralization because N mineralization represents microbial activity and litter fall is a source of organic N substrates. However, there was no relationship between litter fall and N mineralization across our watershed. Additionally, LFC was not correlated with N mineralization, which we also would have expected. It is possible that heterogeneity in the quality of litter inputs or else microclimate-induced rates of decomposition differ over the watershed extent so that no trend was seen in our analysis.

5.5. Sensitivity of Specific DOC Pools to ANPP, But Not Litter Fall or N Mineralization

[37] Additionally, we expected that both extractable DOC content and DOC export would be positively correlated with both ANPP and litter fall. We did find that leached DOC, as measured by lysimeters, significantly increased with increasing ANPP, but was not correlated with litter fall or soil C content. Ecologically, we would also expect relationships between litter fall, SOC, and DOC to exist because litter fall provides approximately 20% of total SOM and 8% of DOC (as measured in a similar temperate stand in Germany) [*Aitkenson-Peterson et al.*, 2006]. Extractable DOC may represent a mix of both old and new soil C, and thus might not be as sensitive to current variation in ANPP as is leachable DOC.

5.6. Potential Gradients in Belowground C Related to Soil Moisture

[38] In complex terrain, environmental conditions can vary on a microtopographic scale and the existence of complex microclimates may affect soil conditions and vegetation [*Daly et al.*, 1994; *Pypker et al.*, 2007]. For example, variation in species composition can affect litter chemistry. Conifer needles are more lignin rich than the broadleaves of deciduous species, so it would be expected that stands consisting predominantly of conifers would decompose more slowly [*Perakis et al.*, 2012]. Additionally, the change in species composition over time means that contributions to the litter and soil C pool integrate over dynamic stand types with different chemistries. Because complex terrain suggests a

highly variable dynamic between environmental conditions, stand composition, and ecosystem functions (particularly decomposition), we found that surprisingly where soil conditions were poor—in warm, dry sites—ANPP would be negatively correlated with LFC and DOC. Our results supported this conclusion and we suggest two possible mechanisms. (1) On very hot, dry sites, extremely low ANPP exists and thus C inputs are correspondingly low. (2) On the steep, exposed slopes where soil conditions are poor on WS1, soil erosion is likely very high, so SOC does not accumulate. In complex terrain, the influence of topography directly on the C content in the heavy fraction was also apparent. Although the sample size was very small, soil type, as well as elevation and slope, was reflected in the C content in the heavy fraction, supporting our hypothesis that HFC would be directly influenced by site characteristics. On WS1, sites at the higher elevations have a different soil mineralogy (andesitic rather than basaltic) than those at lower elevations due to the geologic history of the site [*Swanson and Jones*, 2002] and sites with steep slopes often have very shallow, rocky soils prone to erosion. Both the amount and type of mineral soil affects C content in the heavy fraction.

5.7. Soil Rock Content Thresholds Productivity and C Storage

[39] We expected significant relationships between soil rock content and the ecosystem variables we studied, as rock content can directly affect soil water relations and thus ANPP. Instead, there were almost no significant relationships between ANPP, any SOM pool, or DOC pools with rock content. ANPP, litter fall, and DOC export appear to be lower at relatively high ($> 30\%$) rock contents, but the few observations that we have at high rock content make statistical inference impossible. However, the fact that there was no relationship with ecosystem function at up to 35% rock content was unexpected and suggests that vegetation can adapt to soil heterogeneity and spatially diffuse water resources.

5.8. SOM Integrates Over Inputs From Forest Succession

[40] Site history may also play a key role in how litter fall, ANPP, soil C, and DOC interact on WS1. Harvest documentation notes that after harvest, the north facing slope took well to the replanting of *Psuedotsuga menziesii*, while the south facing slope did not [*Rothacher et al.*, 1967]. Establishment on the south facing slope was dominated by drought-tolerant hardwoods that better tolerate steeper slopes and shallow soils. Species-specific ANPP trajectories confirm this, for example, that the majority of *Prunus emarginata* and *Castanopsis chrysophylla* are found on the south facing slope and have very high productivity at a young age, and they experience maximum ANPP in the first remeasurement interval between 1984 and 1988. North facing slopes, on which conifers initially and currently dominate, reached their maximum in the 1995–2001 remeasurement. Although the north facing slope is currently undergoing canopy closure, its ANPP is still much greater than that on the south facing slope [*Lutz*, 2005; *Lutz and Halpern*, 2006]. Because ANPP looks at the accumulation of all aboveground biomass, not just that which is rapidly turned over, the relationship between litter fall and ANPP may differ by stand type. Although relationships between DBH (as sapwood area) and leaf surface area are positive and well known for many species, both hardwood and conifer [*Meadows and Hodges*, 2002; *Shinozaki et al.*, 1964a, 1964b; *Waring et al.*, 1990], it is also accepted that these relationships are not constant across species or even across trees of the same species but of different morphology, and on WS1 tree heights are highly variable even among the *Psuedotsuga menziesii* alone. On the poorly lit north facing slopes, taller trees predominate, DBH is smaller, number of trees per plot is greater, and biomass is greater than on south facing slopes [*McDowell et al.*, 2008; *Pypker et al.*, 2007]. We suggest that on the north facing slope, positive relationships between litter fall and ANPP on WS1 may be due to greater amounts of heavier (needle) litter, as well as woody turnover, coming from high biomass coniferous stands. On the south facing slopes, where trees are shorter and have less biomass, and hardwoods are more dominant, litter fall measurements may represent rapidly recycling and lighter deciduous foliar inputs.

[41] Litter accumulation may occur when decomposition is limited either by microclimate or by litter biogeochemistry, and thus might obscure direct relationships with ANPP or topography. For example, there are litter mats in exposed parts of the watershed with large populations of *Acer circinatum* on dry, rocky, soils of the south facing slope, where decomposition may be limited by heat and lack of moisture. In contrast, on the north facing slopes of WS1 where soils are moist and deep, coniferous vegetation grows and contains large amounts of decay-resistant coarse woody debris, as well as lignin-rich coniferous needles. In a similar example, *Gholz et al.* [1985] found that *Pinus elliottii* stands that established successfully experienced reduced decomposition rates with age and attributed this to litter chemistry and preferential use of limited soil nutrients by decomposers.

[42] Over complex terrain, soil moisture may be a critical environmental factor in how and where C is stored and lost from soils [*Klute*, 1973; *Nielsen et al.*, 1973]. On WS1, the greatest concentrations of KCl-extractable DOC were found in locations with the greatest upslope area at the basin scale; in general, these are from the lowest elevations and nearest the mouth of the watershed. Not only are these locations saturated for longer periods of time during the year, but they also have highly variable and dense forest communities which contribute to variability in microbial processing and soil incorporation. Exploration of the differences between methods for collecting and extracting DOC showed significant variation between all three methods. One plot, which essentially represents the first-order "pour point" of WS1, had particularly high values of water-extractable and lysimeter DOC. Differences among DOC collections by methods may be attributed to the influence of topography; for example, where soils are highly saturated DOC in the mobile categories (WEDOC and lysimeter leachate) may be increased relative to the available DOC extracted by KCl.

6. Conclusions

[43] While we found that ANPP was correlated with litter fall (increased C inputs) and DOC export, we did not find the expected relationships between ANPP, litter fall, SOM stores per unit area, C content of the soil, or DOC pools. Similarly, soil rock content was not well correlated with ANPP, SOM pools, or DOC export, and only aboveground

productivity decreased at very high (> 30%) percentages of rocks in the upper 50 cm. However, exposed, dry sites had lower SOM stores and content and DOC stores and export than moist wet sites. We conclude that many factors, such as stand history, plant adaptation to drought, and even soil erosion in complex terrain can obscure expected patterns between carbon storage in soils and plant productivity.

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