The effects of topography on forest soil characteristics in the Oregon Cascade Mountains (USA): Implications for the effects of climate change on soil properties

R.P. Griffiths [a,*], M.D. Madritch [a,b], A.K. Swanson [a,c]

[a] Department of Forest Ecosystems and Society, Oregon State University, Richardson Hall, Corvallis, OR 97331, United States
[b] Department of Entomology, University of Wisconsin, 1630 Linden Drive, Madison, WI 53706, United States
[c] Yellowstone Ecological Research Center, 2048 Analysis Drive, Suite B, Bozeman, MT 59718, United States

ABSTRACT

Forest soil measurements were made at over 180 sites distributed throughout the H.J. Andrews Experimental Forest (HJA) in the Oregon Cascade Mountains. The influences of both elevation and aspect on soil variables were measured in the early (1998) and late summer (1994). Increased elevation significantly increased soil moisture, mean annual precipitation, soil organic matter, labile C and mineralizable N, microbial activities, extractable ammonium, and denitrification potentials. In contrast, bulk density, pH and soil temperature (1998 only) were significantly lower at the higher elevations. Relative to labile C, mineralizable N was preferentially sequestered at higher elevations. Aspect significantly affected annual mean temperature and precipitation, soil moisture and temperature, soil organic matter, mineralizable N, extractable ammonium, denitrification, and microbial activities. There were no significant higher statistical interactions between elevation and aspect on climatic or soil factors. Soil organic matter (SOM) accumulation at higher elevations is likely driven by a reduction in decomposition rates rather that an increase in primary productivity, however, SOM accumulation on north facing slopes is probably due to both a decrease in decomposition and an increase in primary production. Models of climate change effects on temperate forest soils based on elevational studies may not apply to aspect gradients since plant productivity may not respond to temperature–moisture gradients in the same way across all topographical features.

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1. Introduction

Predicting global climate change impacts on forest soils posses a significant challenge to forest ecologists and soil scientists. Soils contain vast quantities of sequestered carbon and nitrogen that could potentially be mobilized with global warming and/or changes in precipitation. Both moisture and temperature are known to be primary drivers for plant growth and litter decomposition (Perry, 1994). The balance between these two processes influences the cycling of soil organic matter (SOM) and associated microbial processes (Kirschbaum, 1995).

Current estimates suggest that soils contain approximately three times the carbon found in above-ground biomass and twice that in the atmosphere (Eswaran et al., 1993). Soil warming experiments (Van Clev et al., 1990; Lukewille and Wright, 1997) and measurements along altitudinal and latitudinal gradients (Trumbore, 1997; Garten et al., 1999) have been made to predict the effects of climatic change on soil properties.

A number of studies have addressed the impact of elevation on forest soils in tropical (Schuur and Matson, 2001) and boreal and sub-arctic forests (Sveinbjörnsson et al., 1995; Fisk et al., 1998) but there have been relatively few studies in temperate forests (Morecroft et al., 1992; Kneopp and Swank, 1998) and even fewer in the carbon laden forests of the Pacific Northwest (Powers, 1990). Studies have generally been based on a limited number of sites that provide little or no information about how elevation and aspect influence forest soil properties within the same watershed. In general, these studies have shown that as soils are warmed decomposition rates increase resulting in increased CO_2 production. This effect is especially strong at cooler temperatures where Q_{10} values are greater than those found at higher temperatures (Kirschbaum, 1995).

H.J. Andrews Experimental Forest (HJA) was chosen for a number of reasons: (1) there is approximately 60 years of meteorological, hydrological, biological and silvicultural data for this site which provides a historical perspective to the current study, (2) it is representative of coniferous forests of the Pacific

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* Corresponding author. Tel.: +1 541 737 6559; fax: +1 541 737 1393.
E-mail address: Robert.griffiths@orst.edu (R.P. Griffiths).

Northwest (Greenland, 1994), (3) there is a relatively wide elevation gradient and (4) because of the relatively unpolluted prevailing winds from the Pacific Ocean, nitrogen deposition should be low; this avoids complications caused by high nitrogen deposition rates found in other mountain ranges such as those on the east Coast of the USA (Garten et al., 1999). Within the HJA, there is sufficient topographical variation to impact both mean annual temperature (4.6–9.7 °C) and precipitation (200–317 cm) which either directly or indirectly influenced SOM which ranged from 11.4 to 58.7% (1994) and 7.4 to 58.4% (1998).

The main objective of this study was to measure the effects of both elevation and aspect on forest soil properties. More specifically, our objectives were to demonstrate the effects of topography on the following carbon cycle components; SOM, litter depth, water soluble organic C, labile C, and field respiration as well as the following nitrogen cycle components; mineralizable N, extractable ammonium, and denitrification potentials. Since these factors are all influenced by microbial activity, we measured soil basal respiration rates, substrate-induced respiration (SIR), and β-glucosidase activities. A secondary objective was to measure these variables in a large spatial array over a large mountainous watershed so that krieged data maps of these variables could be generated. It is possible that these spatial arrays would show relationships that were not apparent from standard statistical analyses. At present, there is no similar study published that addresses our research objectives.

2. Materials and methods

2.1. Site descriptions

The HJA is located in the Oregon Cascade Mountains of Western Oregon with a relatively mild Mediterranean climate (Greenland, 1994). Its soils are derived from volcanic parent materials (Sollins et al., 1980) and includes a major drainage basin with elevations ranging from about 500 to >1500 m. Douglas fir (*Pseudotsuga menziesii* [Mirb] Franco) and western hemlock (*Tsuga hetero-phylla*) dominate below 1000 m while Mountain Hemlock (*Tsuga mertensiana* [Bong.] Carr.) and Pacific silver fir (*Abes amabilis*) dominate at elevations above 1000 m (Franklin and Dyrness, 1988). Stand ages ranged from old growth (typically 200–500 years) to recently harvested stands <15 years. When old growth is cut, remaining slash and debris were usually subjected to a light burn, thus leaving burnt stumps and old, decayed logs. These sites are typically replanted within 2 years with Douglas-fir, which represented the majority of trees present in all age classes. Two studies were conducted using essentially the same 180+ locations (Fig. 1). Sample sites were typically located at 0.5-km intervals along all accessible roads forming a sampling array representing all aspects, elevation, soil and vegetation types, and stand ages found on the HJA (Fig. 1). The first study was conducted in August 1994 (late summer) during the hottest and driest season when microbial activity should be at a minimum. The second study was conducted from 15 June to 7 July 1998 (early summer) when soils had higher moisture and were cooler than in August (Tables 1 and 2).

2.2. Sampling techniques

In 1994, one soil sample was collected and one set of field measurements were made at each location. In 1998, multiple samples were taken at 5-m intervals along a 45-m transect parallel to the road. This spacing was chosen because we previously determined from semivariograms that 5-m spacing provided statistically independent samples (Griffiths
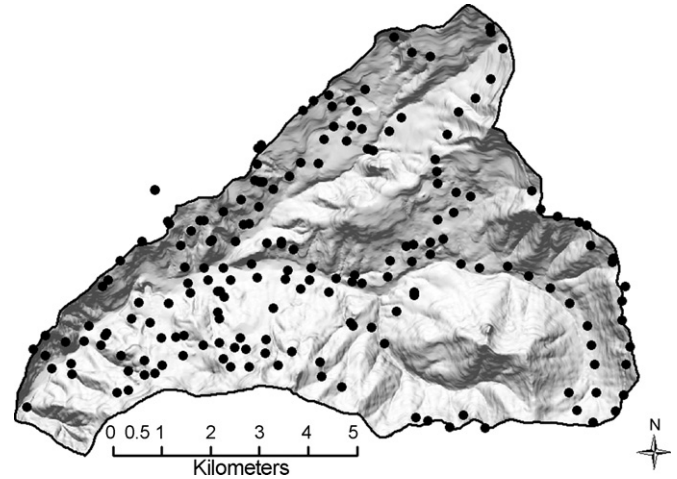

Fig. 1. Sampling locations on a topographical map of the H.J. Andrews Experimental Forest.

Table 1
Effects of elevation on forest floor and soil characteristics; 1994 late summer study

Variable	Units	Elevation		
		Low	Medium	High
Soil temperature	°C	14.5	15.3	14.6
Mean ann. temp	°C	9.2c	8.3b	6.2a
Moisture	%	33.8a	35.0a	48.9b
Mean ann. prec.	cm	217.1a	232.3b	283.8c
pH	pH	5.10b	4.99ab	4.88a
Bulk density	gdm/cm³	0.62c	0.54b	0.46a
SOM	%	19.8a	23.8b	33.2c
WEOC	μgC/gdm	0.47	0.51	0.52
Field resp.	gC/m² day	1.45	1.32	1.53
Labile C	μgC/gdm	218a	238a	388b
Mineralizable N	μmolN/gdm	4.24a	4.64a	6.78b
Labile C:Min N		40.3	42.6	45.8
Extrac. ammon	μmolN/gdm	0.25a	0.30a	0.41b
Basal resp.	μgC/gdm h	0.13a	0.15ab	0.22b
SIR	μgC/gdm h	0.26	0.27	0.37
Denitrification	ngN/gdm h	4.39a	1.54a	7.52b
Alder sites	%	5.3	2.8	5.7

Low, medium and high elevation ranges were <1000 m, 1000–1500 m, and >1500 m, respectively.
Within a row, values that are significantly different at the $p < 0.05$ level are followed by different letters.

Table 2
Effects of elevation on forest floor and soil characteristics; 1998 early summer study

Variable	Units	Elevation		
		Low	Medium	High
Soil depth	cm	29.4	29.8	31.8
Soil temperature	°C	11.8c	10.0b	9.2a
Moisture	%	49.4a	50.8a	75.7c
pH	pH	5.14	5.15	5.14
Bulk density	gdm/cm³	0.84c	0.75b	0.62a
Litter depth	cm	5.3	5.1	4.9
SOM	%	18.7a	21.7b	32.3c
Field resp.	gC/m² day	27.4	25.8	26.3
Labile C	μgC/gdm	281ab	284b	259a
Mineralizable N	μmolN/gdm	6.9a	7.5a	16.4b
Labile C:Min N		39.0a	38.3a	17.1a
Extrac. ammon	μmolN/gdm	0.16a	0.21a	0.91b
β-Glucosidase	μg/gdm h	0.100a	0.118ab	0.122b
Denitrification	ngN/gdm h	3.18a	1.70a	8.48b

Low, medium and high elevation ranges were <1000 m, 1000–1500 m, and >1500 m, respectively.
Within a row, values that are significantly different at the $p < 0.05$ level are followed by different letters.

and Swanson, 2001). Mineral soil depth measurements to bedrock were made at 10 transect locations. Field respiration measurements were made at the center five locations and mineral soil samples were taken from the center three sample locations as 4.7 cm × 10 cm cores and composited for laboratory tests. Litter depth was measured with a cm ruler from the top of the litter layer to the top of mineral soil.

2.3. Field methods (1994)

Aspect, slope, latitude, longitude, elevation, and alder dominance were observed at all sites. Single soil (top 10 cm) and air temperature measurements were taken during two consecutive days in the field using a calibrated dial thermometer. The values reported are the average for the 2 days. Soil samples were collected from the top 10 cm of the forest soil below the litter layer and transported to the laboratory in an ice chest. They were subsequently stored at 15 °C until they were analyzed, usually within 16 h of their receipt.

Field respiration over 24 h was measured using a standard soda-lime technique (Edwards, 1982) in chambers with the soda lime jars elevated approximately 3 cm from soil surface to optimized efficient CO_2 uptake. Chamber walls were seated into the mineral soil to minimize gas exchange with the atmosphere outside of the chamber. Respiration rates reflected those of both forest soil and litter. The only modification to the forest floor within the chamber was the removal of living plant material to eliminate plant CO_2 uptake.

2.4. Field methods (1998)

The following observations were made in the field: litter depth, soil respiration, and soil temperature. Instead of the 24 h soda-lime technique used in the 1994 study, field (forest floor) respiration rates were measured with a nondispersive, infrared CO_2 analyzer (Li-COR®, LI-6200) (Griffiths and Swanson, 2001). Litter depth was measured at the same locations as the field respiration measurements using a cm ruler. Mineral soil depth was measured by driving a calibrated steel rod into the ground. This was done in 10 locations along the above-mentioned transect.

2.5. Laboratory analyses (1994)

Unsieved subsamples were set aside to be used for water extractable organic carbon (WEOC) measurements. Soils were subsequently sieved through a 2-mm sieve for the other analyses. Soil moisture was determined by drying duplicate 10 g field-moist sieved soils at 100 °C for at least 8 h (Griffiths and Swanson, 2001). Soil organic matter was measured by loss-on-ignition at 550 °C for 6 h after oven-drying at 100 °C. Bulk density was measured by oven-drying cores of a known volume. Soil pH was measured in 1:10 (soil:distilled water) slurries of oven-dried (100 °C) soil. These slurries were shaken for 1 h prior to reading pH values with a Sigma model E4753 electrode. WEOC was measured in 5 g of unsieved field-moist soil that was diluted with 15 ml of water in a 100-ml serum bottle. Soil slurries were shaken for 1 h at room temperature and then allowed to stand for 1 h. One and one half ml of the slurry was removed and centrifuged in a microfuge at 11,000 rpm for 5 min. After centrifuging, 0.5 ml of the supernatant was removed, placed in a 0.5 ml centrifuging tube and frozen. Before analysis the samples were thawed and mixed to suspend the precipitate. The samples were analyzed for organic carbon using a Dohrman DC-80 Carbon Analyzer (Dohrman Instruments, Santa Clara, CA). Two blanks containing deionized water were also run with the set.

Laboratory soil respiration rates were measured in three ways using short incubation times. Measurements were made on field-moist unamended soils (basal respiration), soils amended with water and soils amended with glucose. Five grams of field-moist samples were placed in a 25 ml Erlenmeyer flask fitted with a serum bottle stopper. To one, nothing was added, to another, 2 ml distilled sterile water was added and to a third 2 ml of 10^{-3} M sterile glucose (dextrose) solution. The samples were incubated for 1 h and the headspace assayed for CO_2 to account for initial soil disturbance respiration effects and background CO_2 levels. They were incubated for an additional 2 h to determine the actual respiration rate as previously reported by Griffiths et al. (2005). Substrate-induced respiration (SIR) was measured by subtracting water amended from glucose amended soil respiration rates.

Extractable ammonium was determined by shaking 10 g of field-moist soil with 50 ml 2 M KCl for 1 h (Keeney and Nelson, 1982), adding 0.3 ml 10 M NaOH to the slurry, and measuring ammonium concentration in the slurry with an Orion model 95-12 ammonium electrode (Orion Research Inc., Boston, MA). Mineralizable N was measured by the waterlogged technique of Keeney and Bremner (1966) as modified by Griffiths and Swanson (2001). Denitrification potential (DEA) was measured using the method of Groffman and Tiedje (1989) as modified by Griffiths et al. (1998).

2.6. Laboratory methods (1998)

There was an important difference between the methods used to measure labile carbon in the 1994 and 1998. In 1994, the labile carbon determinations were made on field-moist soils. Since these samples were collected during the driest time of the year, moisture was likely limiting respiration in many of the samples. In the 4 years between these studies, we determined that a better measure of labile carbon was possible by standardizing soil moisture. Thus in 1998, all samples were brought to the same moisture content (75%) by adding enough sterile deionized water to equal 3 g water per 25-ml Erlenmeyer flask containing 4 gdm soil. The incubation temperature was increased from 19 °C in the first study to 24 °C in the second to provide a more consistent incubation temperature over 2 weeks. In the 1994 study, no replicate subsamples were processed, but in 1998, all samples were run in triplicate. β-Glucosidase activity was determined by the spectrophotometric assay of Tabatabai and Bremner (1969), as modified by Bonin et al. (2000).

Mean precipitation and air temperatures were estimated for each location using GIS data overlays of mean air temperature and precipitation. The mean annual precipitation (MAP) map was developed by Chris Daly using the PRISM model and is reported as raster digital data accessible from: http://andrewsforest.oregonstate.edu/lter/data/abstract.cfm?dbcode=MS027&topnav=160.

The data used in this model were generated from monthly observations at 15 HJA monitoring sites from 1980 to 1989. These data were modeled at a 100-m grid resolution. The mean annual temperature (MAT) map was developed by Rosentrater (1997). These data are accessible from: http://andrewsforest.oregonstate.edu/lter/data/abstract.cfm?dbcode=MS028&topnav=160. A mountain microclimate simulation model was used to generate a HJA (MAT) data map that we used to estimate MATs for all our sample sites. Monthly mean temperatures collected from 1981 to 1990 from 22 monitoring sites were used in the model. MAT values generated by the model were generally within 0.5 °C of field data (Rosentrater, 1997) Kriged maps were generated from our data using ARC® 8.3 (Environmental Systems Research Institute Inc. Redlands, CA).

2.7. Statistical methods

All statistical analyses were conducted with the PC program Statgraphics® Plus for Windows® (Statistical Graphics Corporation, Rockville, MD). ANOVAs were computed on data from each site since the distance between sample sites was sufficient to insure sample independence as determined by semivariogram analyses (Griffiths and Swanson, 2001). Significance of differences was determined with Fisher's protected least significant difference ($p < 0.05$). SOM, WEOC, basal respiration, mineralizable N, C:N ratio, extractable ammonium, DEA, and β-glucosidase were not normally distributed and were log transformed for the ANOVA. To analyze the data by elevation, sites were grouped as low (∼500–1000 m [$n = 59$]), medium (1000–1500 m [$n = 70$]), and high (>1500 m [$n = 52$]). In the ANOVA aspect analysis, the compass rose was divided into eight equal segments of 45° each. The number of sites within each segment varied by a factor of 3 ranging from 9 to 28 (mean 19 ± 5). A multifactor ANOVA analysis using both elevation and aspect was used to determine if there were any higher-order interactions between elevation and aspect for any of the variables. Correlations between variables were made using Spearman Rank analysis. With one exception, scatter plots of elevation and all response variables showed either linear or no correlations. Denitrification rates showed minimal values at medium elevations. Other than that, no curvilinear or step functions were observed.

3. Results

3.1. Elevation effects on soil properties

In the 1994 (late summer) study, there were no significant elevation differences in soil temperature, WEOC, field respiration rates, labile carbon:mineralizable nitrogen ratios, or percent alder sites (Table 1). When compared with low elevation sites, soil moisture, mean annual precipitation, SOM, labile C, mineralizable N, extractable ammonium, basal respiration, and denitrification potentials were all significantly greater at high elevations (Table 1). Of these, only mean annual precipitation and SOM differed significantly among all three elevation zones. Bulk density and pH were both significantly lower at higher elevations, with bulk density differing significantly among all three elevation zones. Mean annual temperatures and precipitation values for all sites were reported under the 1994 study but they apply to both since the models from which these were derived were estimated from multiyear means (Table 1). These values mirror field measurements for soil temperature in 1998 and moisture in both studies.

There were similarities between the 1994 (early summer) and 1998 (early summer) studies (Tables 1 and 2). Field respiration rates did not differ systematically with elevation in either study even though the methods used were different; soda lime in 1994 and direct measurements using a nondispersive, infrared CO_2 analyzer in 1998 resulting in an order-of-magnitude difference in the estimated rates. In both studies, denitrification potentials were greatest at high elevations, intermediate in the lowest elevations and lowest in the middle elevations although the differences between the lowest and intermediate elevations were not statistically significant. Extractable ammonium concentrations showed essentially the same patterns in both studies, as did SOM, bulk density, mineralizable N, and soil moisture. There were however, three variables that did not show the same trends. In 1994, soil temperature showed no significant differences by elevation but in 1998, high elevation soils were significantly cooler. In 1994, pH differed significantly by elevation with the lowest pHs at the highest elevations. In 1998, no significant differences were

Table 3
Effects of aspect on variables during the 1994 study

Variable	Low value	Aspect	High value	Aspect
Ann. precip.	221	E/SE	280	N
Ann. temp.	7.0	N	9.6	SE
Soil temp.	12.2	N	16.9	S
WEOC	0.23	N	1.14	E/SE
Mineralizable N	5.2	E	8.5	SW
Extr. ammon.	0.28	E	0.59	W
Denitrification	1.4	E/SE	8.6	NW
Basal resp.	0.15	N	0.39	SE
SIR	0	N	0.08	S/SE
% Alder sites	0	Variable	22	N/NE

The values given are the means for all sites in the segment. Only those variables showing significant differences at the 95% confidence level are listed.

Table 4
Effects of aspect on variables during the 1998 study

Variable	Low value	Aspect	High value	Aspect
Soil moist.	48.4	S/SE	69.0	N
Soil temp.	9.8	N/NW	12.1	E/SE
SOM	18.2	E/SE	28.0	W/NW
Labile C:Min N	17.5	W/N	44.2	E/SE
Field resp.	18.0	N	35.5	S
Mineralizable N	5.6	E/SE	17.6	W
Extr. ammon.	0.22	E/SE	0.75	NW
Denitrification	2.0	E	10.7	W

The values given are the means for all sites in the segment. All differences at the 95% confidence level.

seen. In the 1994 study, labile C was highest at the highest elevation, while in 1998, it was lowest at these elevations.

Three variables not measured in 1994 were added in 1998; mineral soil depth, litter depth, and β-glucosidase activity. Mineral soil and litter depth showed no elevational trends but β-glucosidase activity was highest at high elevations.

3.2. Aspect effects

Several variables differed significantly by aspect. Annual precipitation was lowest on E and SE aspects and highest on northerly aspects (Table 3). This did not translate into soil moisture differences in 1994 but did in 1998 (Table 4). Annual mean temperatures were lowest in north facing slopes and highest in SE (Table 3). This trend was also seen in the soil temperatures during both studies. In the 1994 study, SOM showed no significant aspect trends but there were in 1998 where the lowest values were found on E/SE and highest on W/NW aspects (Tables 3 and 4). In 1994, WEOC was significantly greater in E/SE sites than in northern sites (Table 3).

In 1994, field respiration showed no trends but in 1998, the highest rates were found on southerly sites and lowest to the north (Table 4). In both studies, there were significant aspect differences in all nitrogen cycle components. Mineralizable N, extractable ammonium, and denitrification potentials were all lowest in the eastern sites and highest in the north (Tables 3 and 4). The two variables that generally reflect soil microbial activity (basal metabolism and SIR) were lowest in northern sites and highest to the S/SE. A high percentage of alder sites were found on N/NE aspects (Table 3).

4. Discussion

The connection between topographic features (both elevation and aspect) and the primary drivers of temperature and moisture are clearly seen these data. Field measurement of soil temperature (1998) and mean annual air temperatures were lowest at the highest

elevations and northern exposures. Moisture and precipitation were both lowest at the lowest elevations and SE exposure.

4.1. Elevation effects on soil properties

There was a positive link between elevation and SOM with the most significant increase in elevations above 1000 m (Tables 1 and 2); a relationship reported much earlier by Jenny (1980). More recently, Sims and Nielsen (1986) reported the same relationship in Montana mountain soils, as did Garten et al. (1999) in a study of soil carbon pools in the southern Appalachian Mountains. Kane et al. (2005) also reported an inverse relationship between soil organic carbon (SOC) and temperature in black spruce forests of interior Alaska. While estimating the effects of altitude on SOM in 886 data sets across China, Dai and Huang (2006) found a positive correlation between SOM and both MAP and altitude and a negative correlation with MAT. This same result was reported by Homann et al. (2007) using the "Parameter-elevation Regression on Independent Slopes Model (PRISM) to generate climatic data. Soil C and N data was based on 165 and 129 pedons, respectively from each region of 7 regions in the United States. Although most climate studies show a positive relationship between SOM or SOC and MAP, they do no universally show a negative relationship between SOM and MAT (Homann et al., 1995; Liski and Westman, 1997; Callesen et al., 2003; Guo et al., 2006). Several factors may affect the relationship between SOM and MAT. Low MAP values (Guo et al., 2006), fast soil drainage resulting in low soil carbon accumulation and higher net primary productivity at elevated temperatures (Callesen et al., 2003), and forest type in extreme cold climates (Liski and Westman, 1997) may all contribute to a positive correlation.

Reduced temperatures and increased moisture are probably factors responsible for reduced decomposition rates and thus the accumulation of SOM at higher elevations. Decreased soil temperature generally results in decreased litter decay rates (Moore, 1986; Kirschbaum, 1995), soil organic matter decomposition rates (Van Clev et al., 1990; Rustad and Fernandez, 1998) and N mineralization rates (Lukewille and Wright, 1997).

High elevation SOM accumulation might also be due to increased net primary productivity although this seems unlikely. Most studies show decreases in NPP with increasing elevation driven by a shorter growing season (Hansen et al., 2000; Peterson and Peterson, 2001; Peterson et al., 2001; Mäkinen et al., 2002). SOM concentrations can also be influenced by soil depth with shallower soils harboring elevated SOM concentrations (Dimri et al., 1997). Since no significant soil depth trends were observed with elevation, this would not explain the observed SOM patterns.

Bulk density showed an inverse ($r = 0.49$) and soil moisture a direct relationship ($r = 0.73$) with SOM, which has also been reported by (Federer et al., 1993; Amponsah and Meyer, 2000). From this we would predict that with increasing elevation, bulk density would decrease and soil moisture increase, which indeed was the case. Not surprisingly, SOM was also significantly correlated with both labile C ($r = 0.64$) and mineralizable N ($r = 0.75$) in the 1994 study and mineralizable N ($r = 0.52$) in the 1998 study. However, in the 1998 study there was no significant correlation between labile C and SOM ($r = 0.10$). The differing results were likely due to methodological differences. In 1994, labile C was measured in soils at field moisture; in 1998, all soils were brought to a uniform moisture content of 75% so that moisture was potentially limiting in the first study but not the second. The 1994 study was conducted during the driest portion of the year when soil moisture likely limited laboratory soil respiration (Jenny, 1980; Williams et al., 1992). The fact that labile C was correlated with soil moisture ($r = 0.52$) the 1994 study but not in the 1998 study ($r = 0.11$) supports this view.

Even though SOM and mineralizable N showed the anticipated increase with elevation in both studies, labile C did not in the 1998 study, suggesting that there was a relative enrichment of mineralizable or biologically active N over labile C in high elevation soils. This is reflected in reduced labile C:mineralizable N ratios in the 1998 study. On a global scale, total C:total N ratios in cool temperate forests decrease with increasing moisture (Post et al., 1985). Post et al. (1985) estimated total C:total N ratios in moist, wet and rain forests to be 22.5, 20.7, and 15.7, respectively.

Our observed shift in labile C:mineralizable N ratios with elevation is likely due to differences in decomposition rates (Dimri et al., 1997) or to a difference in litter quality (Garten et al., 1999; Bohlen et al., 2001). In an elegant soil transfer experiment conducted at the HJA, Hart and Perry (1999) found when high and low elevation forest soils were incubated in the laboratory under the same conditions, the high elevation soils were enriched in mineralizable nitrogen. This was confirmed in the field where soils transferred from high to low elevations showed annual rates of net N mineralization and nitrification more than double that of soils taken from low elevations. An in situ study of net N mineralization and nitrification rates in closed soil core incubations at different elevations in a Southeastern US deciduous forest showed N mineralization rates to be the greatest at the highest elevations (Kneopp and Swank, 1998). They concurred with Hart et al. (1994) that this trend was driven primarily by substrate quality.

Bohlen et al. (2001) also found that soil C mineralization did not vary with elevation but N mineralization significantly increased. They also found a strong positive correlation between denitrification potentials and nitrate concentrations with elevation. They concluded that topography rather than difference in tree species was the primary driver of soil N cycling. A similar conclusion has been reached by Zak et al. (1991) and Fisk et al. (1998) in studies on the effects of topography on nutrient cycling in a hardwood forest and alpine tundra systems, respectively. They suggest that the increased availability of N in forest soils at higher elevations is related to both decreased litter C:N ratios and reduced N uptake by trees because of relatively slow growth. This would result in a lower demand for inorganic N and an increase in nitrate and DEA. We did not measure soil nitrate concentrations but we did measure DEA, which reflects the relative abundance of mineralized N availability to soil microorganisms over time (Griffiths and Swanson, 2001). Denitrification potentials at elevations above 1500 m were significantly elevated in both of our studies as were extractable ammonium concentrations. In a comprehensive study of soil properties in a hardwood-conifer forest in New Hampshire, nitrate production was positively correlated with elevation and was influenced by tree species (Venterea et al., 2003).

Reduced demand for mineralized N by trees at higher elevations along with the apparent enrichment in mineralizable N in soil organic matter and elevated soil moisture may contribute to the large increase in DEA we observed in elevations greater than 1500 m. It could be argued that since moisture is known to influence denitrification, moisture gradients could explain the denitrification trends with elevation (Groffman and Tiedje, 1989; Verms and Myrold, 1992; Williams et al., 1992). Our data suggests that this is not the case. Mean denitrification potentials for both studies were remarkably similar even though soil moisture was greater in spring (49.4, 50.8, and 75.7 ngN/gdm h) for low, medium and high elevations, respectively than in the summer (33.8, 35.0, and 48.9 ngN/gdm h). In addition mid elevation denitrification potentials were lower than either higher or lower elevations; a trend not observed for soil moisture.

Based on other elevation studies, we anticipated that litter depths would be greatest in higher elevations (Zak et al., 1991; Fisk

et al., 1998) but no significant trends were observed. The fact that litter depths were not significantly different with elevation suggests that net primary productivity and decomposition rates were approximately balanced for this carbon pool.

Litter bag experiments in the Central Cascade Mountains have shown an inverse relationship between litter decomposition rates and elevation based on six sites with approximately the same elevation gradient used in our study (Topik, 1982). If indeed, decomposition rates are reduced, one would expect that microbial activities would show the same trend. They did not. In the 1994 study, basal respiration rates were significantly elevated in the highest elevation zone as were β-glucosidase activities in the 1998 study. There is a possible explanation for this apparent anomaly. Basal respiration and β-glucosidase were measured at temperatures above those found *in situ*. Microorganisms can adapt to the lower temperatures normally found through most of the year at higher elevations. This may result in greater activities when they are exposed to elevated temperatures found at lower elevations (Atlas and Bartha, 1981; Kirschbaum, 1995). If decomposition rates were really elevated at the highest elevations, one would expect that same trend in field soil respiration measurements. This was clearly not the case even though two different measurement techniques were used.

4.2. Aspect effects on forest soils

North facing slopes had higher annual mean precipitation and lower soil temperatures than E/ES facing slopes therefore mimicking high and low elevations, respectively. North–south gradients of annual mean temperature and precipitation were generally translated into gradients of soil moisture and temperature measured in the field along a similar axis. Generally, the same orientation was found for field respiration, WEOC, and microbial activity (basal respiration and SIR) with higher values in S/SE exposure soils and lower values in those facing north. All of these variables are in some way related to decomposition based on extensive literature linking temperature and moisture to organic matter decomposition (Perry, 1994).

It is tempting to assume that the same dynamics drive elevation and aspect-related differences in soil processes. As discussed above, since tree growth tends to decrease with increased elevation, the accumulation of SOM is primarily driven by reduced decomposition. The response of SOM to climatic gradients generated by different aspects may be more complicated since at these latitudes, tree growth may be enhanced by increased moisture on northerly aspects. The influence of temperature and moisture on decomposition rates should be essentially the same in both instances but the same may not hold true for plant production. Light, soil temperature and moisture all influence tree growth and vegetation distribution patterns in a way that may be different depending upon aspect and elevation (Perry, 1994). Coble et al. (2001) found that both gross and above-ground net primary production in Western Montana forests were higher in north facing slopes than those facing south due to a drying trend leading to moisture limitation in the summer months. In a study of the effects of aspect on foliage biomass in a mountainous region of Japan, the highest biomass was also found in the north facing sites (Tatsuhara and Kurashige, 2001). It is likely that the same holds true for the HJA. Thus elevated SOM and other organic pools in N and NW facing slopes may be caused by both a reduction in decomposition and an increase in primary production.

This may explain why maximum/minimum axes for SOM were skewed from the N/S orientation seen for temperature and moisture to toward a more E/W aspect. As a cautionary note, statistically significant SOM distribution patterns by aspect were only seen in the 1998 data. The apparent shift in SOM is therefore based on only one set of observations that does not make a very compelling case for an axis shift. However, three variables with significant SOM rank correlations showed the same orientation; mineralizable N, extractable ammonium and denitrification potentials ($r = 0.75$, 0.42, and 0.43, respectively for 1994 and 0.52, 0.45, and 0.57, respectively for 1998). This suggests that even though decomposition may be driven primarily by the N/S bias of temperature and moisture, SOM input driven by NPP may have been skewed toward E/W.

These data suggest that when attempting to model the impact of climate change in mountains at the basin and larger scales, shifts should be evaluated based on both elevation and aspect since climate gradients associated with these topographic features may not have the same impact on forest soils. It also follows that elevation models based on temperate forests may not apply to mountains at latitudinal extremes because sources and sinks of SOM may not uniformly respond to local climate gradients in the same way. It is interesting that during the ANOVA analysis, there were no significant higher interactions between elevation and aspect for any variables.

5. Conclusions

Studies of forest soils over latitudinal and altitudinal gradients can be used as a point of reference for estimating the effects of climate change on forest soils. We combined a series of soil metrics with geographical data to estimate the effects of climate gradients on forest soil properties on a large watershed. Our observations support other studies which found increased soil organic matter and biologically active nitrogen concentrations at higher elevations. In our study, in contrast to some others, the enrichment of nitrogen at higher elevations was not confounded by concomitant atmospheric N deposition gradients. Through denitrification, the larger pools of organic mineralizable nitrogen at higher elevations could act as potential source of greenhouse gas as the climate warms.

Our data also suggest that climatic gradients generated by elevation and aspect may not influence soils in the same way. Specifically, the mechanism for SOM accumulation may be different. Even though temperature and moisture differences generated from elevation and aspect gradients may have the same effect on organic matter decomposition, this may not be true for plant primary productivity. When modeling the effects of mountain topographic features on soil organic pools, the local influence of aspect on plant productivity needs to be addressed. One of the reasons for the extensive sample array over the HJA was to generate kriged data maps that might show correlations between variables that were not shown by classical ANOVA or correlation analysis. This did not turn out to be the case.

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