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Soil Properties in Old-growth Douglas-fir Forest Gaps in the Western Cascade Mountains of Oregon

Abstract

This was a study of vegetation and soil properties in tree-fall gaps in a coniferous forest of the Pacific Northwest. It had three objectives: (1) to determine if there are correlations between above-ground vegetation and below-ground soil properties within large 50 m diameter gaps, (2) to determine how large gaps influence forest soils compared with non-gap soils, and (3) to measure the effects of differently sized gaps on gap soils. To address these objectives, circular canopy gaps were created in old-growth Douglas-fir forests of the H. J. Andrews Experimental Forest in the western Oregon Cascade Mountains. To address the first objective, within-gap soil spatial patterns were compared with above ground distributions of both vegetation and large woody debris in two large gaps. Spatial and Pearson correlation analyses showed no consistent correlations between soil characteristics and above ground vegetation and coarse woody debris. With reference to the second objective, statistically significant differences between gap and non-gap soil characteristics were observed. Soil moisture, temperature and denitrification potentials were all elevated in forest 50 m diameter gaps and litter depth, labile C, soil respiration, β-gluosidase activity, and ectomytcorrhizal mat concentrations were all reduced. Comparisons between north and south gap soils, showed significant differences in soil characteristics in one but not the other 50 m gap. The third objective was addressed by documenting gap size effects on differences between gap and non gap soil characteristics in two gaps each of 10, 20, 30, and 50 m diameter. Differences between gap and nongap soil moisture, litter depth and ectomycorrhizal mat coverages were essentially the same regardless of gap size. Soil respiration rates and soil organic matter concentrations were similar in 10 m gaps but both lower in gaps 20 m and larger.

Introduction

Tree-fall gaps are known to play an important role in the formation and maintenance of old-growth forest structure and forest biodiversity (Pickett and White 1985, Spies et al. 1990). Prior research has focused on above-ground vegetative succession and population dynamics and little is known about changes occurring below-ground as vegetation becomes reestablished. The interplay between gap microclimatic gradients and both vegetation and the below-ground components of the ecosystem is potentially complex.

Gap formation is known to increase incident light, and soil temperature and moisture (Bauhus 1996, Brockway and Outcalt 1998, Denslow et al. 1998, Gray et al. 2002, Ritter et al. 2005a, Scharenbroch and Bockheim 2007). These are potentially important primary drivers for vegetation establishment, composition and growth (Gray et al. 2002, Gálhidy et al. 2006). Soil temperature and moisture also greatly affect decomposition rates and soil processes (Wagner and Wolf 1998). In addition to gap-canopy gradients, abiotic variables are influenced by location within gaps (N-S gradients and edge effects) as well as gap size (Dirzo et al. 1992, Bauhus and Bartsch 1995, Zhang and Zak 1995, Bauhus 1996, Denslow et al. 1998, Wright et al. 1998, Gray et al. 2002, Ritter et al. 2005a, Gálhidy et al. 2006, Walters et al. 2006).

It is also known that gap size can influence the degree to which gap soils and vegetation are altered relative to the surrounding forest (Dirzo et al. 1992, Parsons et al. 1994a, Zhang and Liang 1995, Zhang and Zak 1995Gray and Spies 1996, Denslow et al. 1998, Gray et al. 2002, Gálhidy et al. 2006,). As gap size increases, gap microclimate gradients increase and the effects of surrounding vegetation on both above and below ground variables are reduced. After gap formation, both microclimate and soil legacies influence the type and growth of pioneer vegetation (Perry et al. 1989, Gray and Spies 1996). In theory, vegetation should impact forest soils through a feedback loop with vegetation acting as a sink or source of soil nutrients and a source of organic compounds from both detritus and direct input via fine roots (Perry

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1994). In fact, there are many studies which have shown the impact of different tree species on forest soils (Tarrant and Miller 1963, Van Miegroet and Cole 1985, Homann et al. 1992, Ogden and Schmidt 1997, Griffiths et al. 1998, Erickson et al. 2005). To our knowledge, there have been no attempts to compare within gap vegetation patterns with patterns of soil processes within the same tree gaps. This study is a companion to others that have been reported on both the microclimate and vegetation distribution patterns in the same 50 m gaps reported here (Gray and Spies 1996, 1997; Gray et al. 2002).

The few studies that have focused on temperate forest gap soil characteristics have measured relatively few variables such as respiration, microbial biomass and nitrogen cycling. To provide a more complete picture of how forest gaps influence soil properties, we chose to measure soil organic matter (SOM), soil temperature and moisture, litter depth, labile C, field respiration in mineral soils, β-glucosidase activity, dentrification potential (DEA), and the coverage of two ectomycorrhizal mat types These variables were chosen because soil temperature and moisture can influence soil processes and plant growth. SOM, labile C, litter depth, and field soil respiration rates are all indicators of forest soil carbon pools and C biogeochemical cycling rates. β-glucosidase activity is a microbial activity indictor. DEA is an indicator of mineralized N availability; and mycorrhizal mats are known to play an important role in soil nutrient cycling. In addition to these below-ground and forest floor variables, the following above-ground variables were determined: herb and shrub biomass, trees larger than 5 cm dbh, total biomass, large wood cover and old stump cover. Analyses of these variables were useful in addressing the following objectives: (1) to determine if there are correlations between above-ground vegetation and below-ground soil properties within a large 50 m gap, (2) to determine how large 50 m gaps influence forest soils compared with non-gap soils and (3) to measure the effects of different sized gaps on gap soils.

Methods

Experimental Design

The gaps studied for this paper were created in an old growth (overstory trees approximately 500 years of age) Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco)-western hemlock (*Tsuga heterophylla* (Raf.) Sarg.) stand in the fall of 1990 (Gray and Spies, 1996). The stand was located at 44° 15′ N, 122° 15′ W at an elevation of 900 m at the H.J. Andrews Experimental Forest (HJA) in the Central Oregon Cascade Mountains. Mean annual air temperature and precipitation from the nearest station (HJA WS2, 8 km west of the study site) was 8.6 °C and 224 cm, respectively. The plant community most closely resembled the western hemlock/rhododendron-dwarf Oregon grape association (McCain and Diaz 2002). Two gaps each of four different sizes were created that were 10, 20, 30, and 50 m in diameter between crown drip-lines, roughly circular, and on relatively flat ground (slope <20%).

Two experimental designs were followed**.** To address our main objective, the spatial distribution of soil variables, vegetation, and surface substrates was measured within and around the two 50 m diameter gaps. Sampling was done on a 4 m grid oriented north-south across each gap and that extended 12 m into the adjacent forest, resulting in over 250 samples per gap. Each day samples were collected on complete transects so that there was no sampling bias introduced for gap and non gap, N versus S, and edge versus center samples. The data were collected 9 years after gap formation, from 25 June to 18 July 1999. Although both gaps were generally circular, there were irregularities in the gap; the actual outlines of overstory tree crowns were used to classify sample points as within or outside of each gap.

To assess the effect of gap size on soil properties, observations were made at two different times on the each of the duplicate 10, 20, 30 and 50 m diameter gaps. The first observations were made from mid July to mid August 1995 (5 yr post-cutting) with additional observations and sampling in July 1997 (7 yr post-cutting). Sampling was conducted at 1 m intervals on north-south and east-west transects that ran through the center of each gap and continued one radius length into the adjacent forest on both ends of each transect. Soil samples from each transect were collected during the same day.

Field Measurements and Sampling

The following measurements were made in the field: litter depth, field mineral-soil respiration, ambient light, soil temperature, percent mycor-

rhizal mat coverage within each core, vegetation cover and size, and coarse woody debris size. Litter depth was measured with a ruler to the mineral soil. Field (mineral soil) respiration rates were measured with a nondispersive, infrared CO_2 analyzer (LI-6200; LI-COR Biosciences, Lincoln, NE). Measurements were made over a period of 1 min after the chamber gas reached ambient CO_2 concentration. The instrument was calibrated on site against a known standard at each location. A Q_{10} adjustment was made for ambient soil temperature. Light was measured with a LI-COR photometer. Soil temperature was measured by dial analog thermometers calibrated at 0 °C with ice water. The temperature probes were inserted into the mineral soil to a depth of 10 cm. In both studies, one 4.7 x 10 cm core was collected at each site, sealed in a plastic bag and kept in an ice chest until it could be returned to the field laboratory where it was stored at 15 °C until the soil was processed (usually within 16 hr). The distribution of ectomycorrhizal mats was determined visually in the field by inspecting the relative abundance of mats in each 4.7 x 10 cm core before it was placed in a plastic bag. When the core was viewed from above, the area covered by fungal mats was estimated. Two distinct mat types were scored: (1) mats similar to those of the genus *Hysterangium* and (2) mats similar to those of the genus *Gautieria*. This approach has been used successfully in the past to document ectomycorrhizal mat distribution patterns in coniferous forests of the Pacific Northwest (Griffiths et al. 1996).

Vegetation was measured in nested 0.25 m^2 and 3.14 m^2 plots around each 4 m grid soil sample point in the 50 m gaps. Forbs, shrubs, and trees < 1 m in height were measured in the smaller plot, shrubs and trees > 1 m in length and < 5 cm diameter at breast height (dbh; 1.37 m) were measured in the larger plot. Cover of each species was estimated and basal diameters (at the ground line) of stems of selected woody species were determined. The cover and diameter measurements were used to calculate biomass (Means et al. 1994), which was summed by lifeform (i.e., tree, shrub, forb) for each grid point. Locations and sizes of trees >5 cm diameter, stumps from cut trees, and large wood pieces ≥ 10 cm in diameter and ≥1 m in length (all decay classes) were sketched in reference to grid locations in and around the gaps and data digitized in a geographic information system (GIS). Elevation was measured within and around each large gap at 8m intervals with survey instruments.

Laboratory Measurements

In preparation for laboratory analyses, all mineral soils were sieved through a 2-mm sieve. Soil moisture was determined by drying duplicate 10 g field-moist sieved soils at 100 ºC for at least 8 hr. Percent soil moisture was calculated by dividing the difference between wet and dry samples by dry wt. then multiplied by 100. Soil organic mater (SOM) was measured as weight loss after ignition at 550 ºC for 12 h on soils that had been dried at 100 ºC for 12 h.

Duplicate laboratory respiration measurements were made on soils brought to 75% moisture content by the addition of enough sterile deionized water to equal 3 g water per 4 gdw soil. Once sealed with serum bottle stoppers, 25-mL Erlenmeyer flasks were incubated at 24 ˚C for 14 days after which headspace CO_2 concentrations were measured by injecting 0.5 ml headspace gas into a Hewlett Packard model 5890 gas chromatograph (GC) fitted with a flame ionization detector in series with a methanizer. The GC was connected to a Hewlett Packard model 3396 integrator to estimate CO_2 concentrations and was calibrated by the external calibration method with known gas standards.

β-glucosidase activity was determined by the spectrophotometric assay of Tabatabai and Bremmer (1969), as modified by Zou et al. (1992). One mL of 10 mM p-nitrophenyl β-D glucopyranoside substrate was added to duplicate 1-mL subsamples containing a soil slurry (1 gdw in 1 mL deionized H_2O). The tubes were shaken and then placed with duplicate controls without substrate in a 30 °C water bath for 2 hr. After incubating, 1 mL of 10 mM p-nitrophenyl β-D glucopyranoside was added to the controls, and all reactions were immediately stopped by the addition of 2 mL of 0.1 M tris[hydroxymethyl]aminomethane at pH 12.0. The mixtures were centrifuged for 5 min at 500 x g. From the supernatant, 0.2 mL was diluted with 2.0 mL deionized water. The optical density was measured at 410 nm, and a standard curve was prepared from 0.02 to 1.0 µmol/mL p-nitrophenol (pNP). Duplicate aliquots and controls were run for all samples.

Duplicate denitrification potential measurements were made using a method by Groffman and Tiedje (1989) as modified by us (Griffiths et al. 1998). Each reaction vessel (25-mL Erlenmeyer flask) contained 5 g of <2 mm, field-moist soil. Flasks were sealed with rubber serum bottle stoppers and purged with Ar to displace O_2 in the headspace gas. After purging with Ar, 2 mL of a solution containing 1mM each glucose and NO_3^- was added to each flask. After the flasks had been incubated at 24 °C for 1 h, 0.5 mL of headspace gas was removed from the reaction vessel and injected into a gas chromatograph (GC) fitted with an electron capture detector (Hewlett Packard model 5890 GC connected to a Hewlett Packard model 3396 integrator). This provided a baseline time 0 reading. Extensive experimentation with this technique conducted by us has shown that a 1 hr preincubutation period is required to establish a consistent N_2O release rate (Griffiths, unpublished data). A second headspace N_2O analysis was made after an additional 2-h incubation. Net N_2O released over this 2-h period was used to estimate N_2O production rates.

Statistical Analyses

Vegetation, surface, and soil variables for each 50 m gap were examined in GIS to search for visual patterns of association. The area covered by large wood and old decayed tree bases ("stumps") in 1 m radius circles around each 4 m grid point was calculated in GIS. Elevation surfaces were generated from measurements using kriging and the estimated elevation of each grid point was extracted. Spatial analyses were made in ARC 8.3 (Environmental Systems Research Institute Inc., Redlands, CA). Correlations between individual aboveground and belowground variables for each 4 m grid point were calculated using Pearson correlation coefficients

Each 50 m gap was treated separately because there were insufficient degrees of freedom to represent the repeated measures of locations within each gap in a combined analysis, and because initial analyses indicated the responses in the two gaps were different. Separate single-factor analyses of variance were used to test for differences in soil attributes in and outside of gaps, the north and south sides within gaps, and the centers and edges within gaps using Statgraphics (Statistical Graphics Corporation, Rockville, MD). Edges were defined as grid points within 6 m of the canopy outline of each gap, while centers were >6 m from gap edges. In most cases, the significance of difference was at the $P < 0.001$ level. Differences at the $P<0.05$ level were considered significant; choosing a less conservative level (e.g., $p<0.10$) could be justified by the high inherent variability of soils, but had little effect on interpretation of results in this study. SOM and soil moisture were normally distributed. All other variables were log transformed prior to analysis.

The effect of gap size on soil variables was tested with a mixed model ANOVA with a split-split plot design. For each replicate of gap size, sample location (in vs. out) was the first split, and year of measurement (1995 vs. 1997) was the second split (with only 2 years of data, the split plot analysis is identical to repeated measures). The effects of measurement year were presented in the ANOVA results but were not of interest and not discussed further. Litter depth and lab respiration were log-transformed to meet assumptions of equality of variance, but transformation was not needed for the other variables. Least-squared means and standard errors were calculated within the model for the main effects, and differences among means were assessed with the Tukey adjustment at the $P<0.05$ level (LSMEANS statement, MIXED procedure, SAS Institute, 2002).

Results

Comparisons Between Above and Below Ground Variables

No consistent trends were observed for any of the variables measured above and below ground. A correlation analysis confirmed our initial observations (Table 1). Although there were some significant correlations between above and below ground variables for individual gaps, these correlations were not consistent between two 50 m gaps. In cases where there were significant differences, the correlation coefficients were generally low. The number of significant correlations (eight) were not too different from the Type I error rate of 90 different tests at alpha=0.05.

Large Gap Study

With the exception of SOM concentrations, in gap 1, all variables in both gaps were significantly different at the $P = 0.001$ level from non-gap soils (Table 2). Soil moisture and temperature, and

TABLE 1. Pearson correlation coefficients between above and below ground variables. The correlations shown in bold had p values < 0.05. The number of observations in Gaps 1 and 2 were 114 and 122, respectively.

	Moist	Temp	Litter	Labile C	Soil resp	Bgluc.	Denit	Hyster	Gaut
Gap 1									
Herb biomass	0.12	-0.17	-0.06	-0.01	-0.09	-0.02	0.05	-0.12	-0.08
Shrub biomass	0.09	0.01	-0.07	0.00	-0.07	0.02	0.05	-0.10	-0.05
Tree biomass (<5 cm dbh)	-0.03	0.04	0.02	**-0.19**	-0.05	-0.06	0.00	-0.04	-0.05
Total biomass	0.12	-0.09	-0.08	-0.06	-0.11	-0.05	-0.06	**-0.15**	-0.10
Elevation	0.05	**-0.16**	0.05	-0.09	0.03	0.04	-0.02	0.10	-0.09
Large wood cover	0.03	0.06	-0.05	-0.02	-0.06	-0.03	0.07	0.03	-0.09
Old stump cover	-0.01	-0.02	-0.04	0.00	-0.01	-0.04	-0.02	-0.03	0.02
Gap 2									
Herb biomass	0.21	0.12	-0.15	-0.13	-0.04	-0.01	**0.30**	0.07	-0.12
Shrub biomass	-0.07	-0.26	0.27	-0.24	0.11	-0.18	-0.11	0.24	0.07
Tree biomass (< 5 cm dbh)	0.03	-0.07	0.05	0.13	0.08	-0.07	-0.04	-0.03	**0.43**
Total biomass	0.05	-0.17	0.20	-0.24	0.08	-0.16	0.04	0.21	0.08
Elevation	0.12	0.01	**0.25**	0.10	-0.05	0.04	0.12	**0.17**	0.07
Large wood cover	0.04	0.08	-0.10	0.01	**-0.15**	0.05	0.05	0.09	0.05
Old stump cover	0.03	-0.21	0.20	0.20	0.18	0.14	-0.26	0.00	0.00

Abbreviations: Moist = Soil moisture; Temp = Soil temperature; Litter = Litter depth; Labile C = Labile carbon; Soil resp = Soil respiration; Bgluc = β-glucosidase; Denit = Denitrification potential; Hyster = Hysterangium-like ectomycorrhizal mat; Gaut = Gauteria-like ectomycorrhizal mat

TABLE 2. Means and significance of difference between sites within and outside gaps. Standard error values are given in parentheses after the means. The F-statistics for each test are shown (numerator df=1); variables with different letters were significantly different at $P < 0.05$. Sample sizes for Gap 1 were 114 and 139 respectively, for gap and non-gap soils; for Gap 2 n = 122 and 137 respectively, for gap and non-gap soils.

Variable	Units	F-value	Gap		Non-gap	
Gap 1						
Soil Moisture	%	4.2	79.2	(3.8)a	68.2	(3.8)b
Soil Temp	° C	20.6	10.4	(0.16)a	9.5	(0.12)b
Soil Organic Matter	%	2.5	30.6	(2.4)	34.4	(1.5)
Litter Depth	cm	42.3	1.65	(0.16)a	2.60	(0.14)b
Soil Labile Carbon	µg/gdw	13.8	1.13	(0.04)a	1.35	(0.04)b
Soil Resp	gC/m3-day	22.4	16.6	(1.2)a	23.4	(1.5)b
Soil β-Glucosidase	µg/gdw-hr	24.4	0.28	(0.01)a	0.38	(0.02)b
Soil Denitrification	ng/gdw-hr	9.5	7.62	(0.84)a	4.06	(0.51)b
Gautieria Mat Cover.	%	29.2	0.37	(0.14)a	6.12	(1.33)b
Hysterangium Mat Cover.	%	27.1	4.84	(1.02)a	11.4	(1.44)b
Gap 2						
Soil Moisture	%	4.4	77.1	(2.8)a	69.4	(2.4)b
Soil Temp	° C	54.5	11.5	(0.2)a	9.7	(0.2)b
Litter Depth	cm	83.3	1.64	(0.06)a	2.61	(0.08)b
Soil Labile Carbon	µg/gdw	19.6	1.29	(0.05)a	1.56	(0.04)b
Soil Resp	gC/m3-day	24.1	17.9	(1.0)a	24.4	(1.2)b
Soil β-Glucosidase	µg/gdw-hr	12.0	0.29	(0.01)a	0.37	(0.01)b
Soil Denitrification	ng/gdw-hr	24.7	16.1	(1.8)a	8.4	(0.7)b
Gautieria Mat Cover	%	7.6	0	(0)a	2.20	(1.0)b
Hysterangium Mat Cover.	%	44.7	0.35	(0.15)a	4.61	(0.80)b

TABLE 3. Means and standard errors of variables (in parentheses) in north and south side of both 50 m gaps. Only samples collected within the bounds of the gap were used in this analysis. The F-statistics for each test are shown (numerator df=1); variables with different letters were significantly different at $P < 0.05$. Sample sizes for Gap 1 were 59 and 55 respectively, for north and south sectors; for Gap 2 n = 72 and 50 respectively, for north and south sectors.

Variable	Units	F-value	North		South	
Gap 1						
Light	µmoles/sec	12.9	90.3	(26.2)a	29.5	(8.0)b
Soil Moisture	%	9.2	70.0	(2.9)a	92.6	(7.9)b
Soil Temp	° C	43.7	11.1	(0.2)a	9.4	(0.2)b
Litter Depth	cm	0.6	1.55	(0.18)	1.78	(0.31)
Soil Labile Carbon	µg/gdw	5.8	1.04	(0.06)a	1.24	(0.06)b
Soil Resp	gC/m3-day	17.4	13.5	(1.2)a	24.5	(2.1)b
Soil β-Glucosidase	µg/gdw-hr	19.5	0.21	(0.01)a	0.30	(0.02)b
Soil Denitrification	ng/gdw-hr	1.3	7.3	(1.1)	8.2	(1.2)
Gautieria Mat Cover.	%	0.7	0.28	(0.17)	0.50	(0.26)
Hysterangium Mat Cover.	%	3.2	3.89	(1.30)	6.20	(1.68)
Gap 2						
Light	µmoles/sec	0.0	24.2	(3.1)	25.1	(3.9)
Soil Moisture	%	0.0	77.4	(3.7)	76.5	(4.3)
Soil Temp	° C	3.3	11.8	(0.3)	11.1	(0.3)
Litter Depth	cm	0.0	0.95	(0.08)	0.96	(0.09)
Soil Labile Carbon	µg/gdw	1.8	1.33	(0.06)	1.22	(0.08)
Soil Resp	gC/m3-day	0.3	18.8	(1.1)	21.2	(2.0)
Soil β-Glucosidase	µg/gdw-hr	2.5	0.27	(0.01)	0.24	(0.01)
Soil Denitrification	ng/gdw-hr	0.4	16.1	(2.6)	16.1	(2.0)
Gautieria Mat Cover.	%	0.0	0	(0)	0	(0)
Hysterangium Mat Cover.	%	1.0	0.43	(0.20)	0.22	(0.22)

denitrification potential rates were all significantly greater in gap than in non-gap soils. Even though the reduction in gap SOM was not significant it followed the same trend seen in the gap size study described below. Litter depth, labile C, soil respiration, β-glucosidase, and ectomycorrhizal mat coverages were all significantly lower in these two 50 m gaps when compared with the surrounding forest.

In addition to the gap-nongap comparisons, we wanted to determine how within gap location influenced soil characteristics. In gap 1, comparisons between north and south sector gap samples showed significant reductions in soil moisture, labile C, soil respiration, and β-glucosidase activities in northern gap soils (Table 3). Soil temperature was significantly elevated. Although not statistically significant, light levels appeared to be about 3 x higher in the northern sector and a reduction in mat coverage was suggested in the same sector when compared to those in the south. In gap 2, none of these differences were observed (Table 3).

It is also possible that there might be an edge effect in large gaps. In the 50 m gap that showed significant north-south gradients described in Table 3, we compared soil values found within 6 m of the edge with those in the center of the gap. No significant differences were observed (Table 4).

Gap Size Study

Soil organic matter (SOM) was essentially the same in 10 m gap and non gap soils (Figure 1a). In the larger gaps, gap SOM was less than in non gap soils. These differences were consistent but not statistically different at the $P \leq 0.05$ level (Table 5). A similar trend was observed for soil respiration rates (Figure 1b) with significant differences across all gap sizes and a suggested gap size by position interaction (P=0.067, Table 5). In contrast to this pattern, a significant interaction effect indicated that litter depth was lower in 50 m gaps than in non gap soils (Figure 1c). Litter depth in gap soils was significantly lower in the smallest gap as well but the largest differential was observed in the 50 m gaps. Soil moisture was significantly higher and mycorrhizal mat coverages significantly lower in gaps when compared with non-gap soils for all gap sizes, with the largest observed difference for mats in the 30 m gaps (Figures 1d and 1e).

TABLE 4. Means and standard errors for those sites in the center of Gap 1 and those that were within 6 m of the edge. The F-statistics for each test are shown (numerator df=1); none of the variables showed significant differences. Sample sizes were 71 and 51 respectively for center and edge.

Variable	Units	F-value	Center		Edge	
Light	µmoles/sec	1.5	53.5	(12.9)	81.8	(31.6)
Soil Moisture	%	0.4	81.5	(5.3)	76.1	(5.3)
Soil Temp	° C	0.3	10.3	(0.2)	10.5	(0.2)
Litter Depth	cm	2.3	1.60	(0.26)	1.71	(0.20)
Soil Labile Carbon	µg/gdw	2.6	1.10	(0.5)	1.17	(0.06)
Soil Resp	gC/m3-day	1.1	18.4	(1.7)	17.5	(1.7)
Soil β-Glucosidase	µg/gdw-hr	0.4	0.24	(0.01)	0.25	(0.02)
Soil Denitrification	ng/gdw-hr	0.8	7.04	(1.13)	8.44	(1.26)
Gautieria Mat Cover.	%	0.3	0.42	(0.18)	0.30	(0.23)
Hysterangium Mat Cover.	%	2.9	3.9	(0.9)	6.4	(1.9)

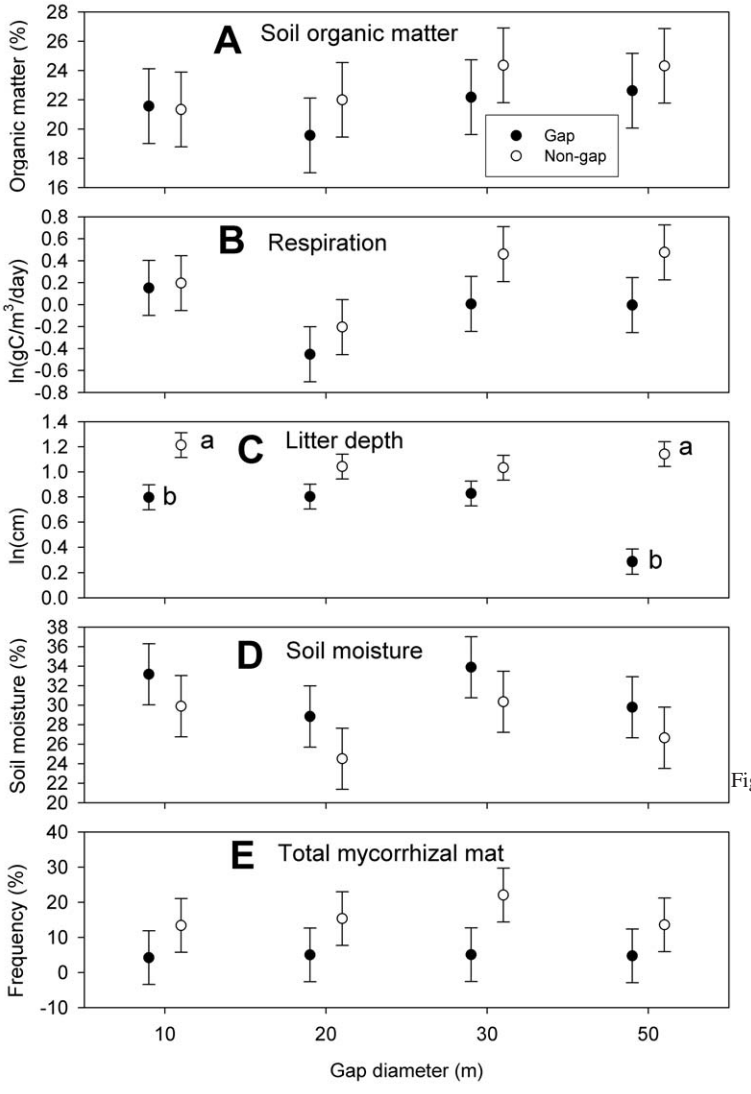

Figure 1. Mean and standard errors bars for selected soil variables in and outside 10, 20, 30, and 50 meter diameter gaps: A, soil organic matter; B, soil respiration; C, litter depth; D, soil moisture; and E, total mycorrhizal mat coverage. Standard errors of the mean were generated by least-squared means within the statistical model; different letters next to observations in a pair indicate a significant difference ($p<0.05$).

TABLE 5. Results of split-split plot ANOVA on effects of gap size and location in and outside of gaps for selected soil variables. Mycorrhizal mats were measured in one year.

	Soil organic matter				Respiration			
Source	d.f.	MS	F-value	$P \geq F$	d.f.	MS	F-value	$P \geq F$
Gap size	3	14.16	0.3	0.835	3	0.60	1.2	0.410
Error: rep x gap size	4	49.68			4	0.49		
In/out	1	18.51	7.4	0.053	1	0.75	49.8	0.002
Gap size x In/out	3	2.90	1.2	0.429	3	0.08	5.5	0.067
Error: rep x gap size x In/out	4	2.50			4	0.02		
Year	1	29.44	3.3	0.108	1	0.19	3.1	0.115
Gap size x Year	3	3.65	0.4	0.752	3	0.46	7.7	0.010
In/out x Year	1	8.15	0.9	0.368	1	0.00	0.0	0.872
Gap size x In/out x Year	3	3.19	0.4	0.787	3	0.01	0.1	0.954
Error: Residual	8	8.97			8	0.06		
Total	31				31			

	Litter depth				Soil moisture			
Source	d.f.	MS	F-value	P ≥ F	d.f.	MS	F-value	P ≥ F
Gap size	3	0.13	1.9	0.273	3	54.88	0.7	0.582
Error: rep x gap size	4	0.07			4	74.31		
In/out	1	1.47	128.5	0.000	1	102.07	23.5	0.008
Gap size x In/out	3	0.18	15.6	0.011	3	0.56	0.1	0.938
Error: rep x gap size x In/out	4	0.01			4	4.34		
Year	1	12.82	85.8	0.000	1	290.44	11.6	0.009
Gap size x Year	3	0.22	1.4	0.302	3	44.76	1.8	0.226
In/out x Year	1	0.04	0.3	0.627	1	28.93	1.2	0.313
Gap size x In/out x Year	3	0.14	0.9	0.467	3	8.27	0.3	0.803
Error: Residual	8	0.15			8	24.96		
Total	31				31			

	Total mycorrhizal mat			
Source	d.f.	MS	F-value	P ≥ F
Gap size	3	18.84	0.1	0.955
Error: rep x gap size	4	186.61		
In/out	1	512.01	11.0	0.030
Gap size x In/out	3	14.47	0.3	0.818
Error: Residual	4	46.66		
Total	15			

Discussion

Abiotic Variables

In both 50 m diameter gaps, soil temperature and moisture were significantly elevated compared with non-gap soils. This was confirmed by a much more comprehensive study of abiotic variables in these and three other sets of gap treatments made at the Wind River Experimental Forest in the southern Cascade Mountains of Washington state (Gray et al. 2002). Similar results have also been reported by Bauhus (1996), Brockway and Outcalt (1998), Denslow et al. (1998), Ritter et al. (2005a), Scharenbroch and Bockheim (2007). Although both sets of measurements were made in the middle of the summer, the trends were typical for gap microclimatic gradients found during much of the growing season (Gray et al. 2002, Griffiths and Filan 2007). Compared with the surrounding forest, increased soil moisture in gap soils is thought to be caused by decreased water demand by plants (Gray et al. 2002).

Others have reported gap N-S microclimatic gradients (Canham et al. 1990, Bauhus and Bartsch 1995, Bauhus 1996, Gray et al. 2002). In gaps larger than 10 m within two years of gap formation, Gray et al. (2002) found significantly higher solar radiation levels in the north sides of the gaps which translated into warmer soils. Microclimatic differences increased with increased gap size. In 10 m gaps, microclimatic variables were essentially the same as surrounding forests. The north-south gradient in the northern temperate latitudes is caused by the sun angle in the southern sky resulting in a shadow being cast by the surrounding forest into the south end of the gap and radiation reaching the forest floor on the north side. Due to tree height in these mature conifer forests, gaps 10 m and smaller have essentially the same microclimatic régime as the surrounding forests.

In one of our 50 m gaps (gap1), soil moisture in northern gap soils was significantly reduced compared with moisture in southern soils. Soil temperature showed the reverse trend. Similar results have been reported by Bauhus and Bartsch (1995) in their study of Beech forest gaps. We did not find the same gradients in the second 50 m gap (gap 2). It is likely that differences in slope and aspect within the gap may account for the differences in gradient among the gaps. The second gap was uniformly southwest-facing with a 21% slope, which may have resulted in similar exposure to afternoon solar radiation across most of the gap. In contrast, the first gap had a convex shape over most of the northern end and a concave shape at the south end, possibly contributing to the warmer and drier conditions in the north.

The only abiotic variable measured in the gap size study was soil moisture. Soil moisture was significantly higher in gap than in non gap soils across all sizes. Others have reported similar results. Soil moisture was significantly elevated in both large (35-40 m) and small (10-15 m) European beech forest gaps (Gálhidy et al. 2006). In their study of varying gap size effects in a tropical wet forest, Denslow et al. (1998) found elevated soil moisture and temperature in gaps of varying sizes. They suggested that elevated gap moisture is caused by a reduction in evapotranspiration most probably related to reduced fine root mass. More recently Scharenbroch and Bockheim (2007) also reported elevated moisture in smaller (≤10 m gaps) northern hardwood-hemlock forests.

Carbon Dynamics

Light, moisture and nutrient gradients are all major factors affecting the establishment and growth of vegetation in gaps (Denslow et al. 1998, Gálhidy et al. 2006) with the interplay between light and soil moisture being key to forest gap regeneration (Dai 1996, Gray and Spies 1997). Gap light and microclimatic gradients that interact with vegetation regrowth are influenced by both gap size and age (Brokaw and Scheiner 1989, Dirzo et al. 1992). Understory forbs and shrubs increase in abundance soon after gap formation, including pioneer species which are rare within undisturbed areas in forests; these species often have different litter qualities and mycorrhizal associates than the dominant vegetation in the surrounding forest. Because of feedback loops between vegetation and soils (Perry 1994), we predicted that gap vegetation gradients would influence soil carbon levels. When maps of vegetation biomass by life form and coarse woody debris in 50 m diameter gaps were compared with soil characteristic patterns, no obvious correlations were found. This may have been due to either the scale of sampling or the size of vegetation clumps. At the 4 m sampling resolution used in this study, it is possible that naturally occurring heterogeneity was too high to show trends related to vegetation patches. In a study of young-old growth edges, we found depressions in carbon pools within 10 m of the edge using a 1 m sampling grid that would not be found at 4-5 m (unpublished data). Using a 4 m sampling grid in this study, no edge effect was found even though one would have predicted it from the edge study. This supports the hypothesis that the sample intensity was not sufficient to pick up correlations between above and below ground components.

Even though we found no correlations between vegetation and soil characteristics, there were patterns in gap carbon cycles. In the largest gaps, litter depth was significantly reduced suggesting reduction of carbon input to soils by litter fall. It is also likely that harvesting overstory trees also reduced soil carbon input through fine roots, which can input a significant amount of carbon into soils (Taskinen et al. 2003, Brunner and Godbold 2007). In both of the 50 m diameter gaps, we found significant reductions in soil respiration (about 28%). Reduced soil respiration rates were also observed in gaps larger than 10 m. Similar soil respiration reductions were observed by Ma

et al. (2005) while comparing open canopy and closed canopies in a California old-growth mixed-conifer forest.

Forest soil respiration rates include both root respiration and soil organic matter decomposition rates and are thought to reflect relative forest primary productivity (Williams et al. 1997, Law et al. 1999). Although soil respiration rates initially increase due to soil disturbance and root decomposition (Peng and Thomas 2006), soil respiration in gaps may decrease in time as roots decompose, new roots have yet to be reestablished and litter decreases because of reduced vegetative productivity. Such a depression in respiration rates was observed by Brumme (1995) in two–year-old 30 m beech forest gaps. He concluded that this reduction was due to a reduction in root respiration. Others have reported reductions in fine root biomass in tropical wet forest gaps (Silver and Vogt 1993, Ostertag 1998) and fine root growth in temperate beech forest gaps (Bauhus and Bartsch 1996). Very few fine roots were observed between 5 m from inside the gap edge and the center of 50 m diameter gaps in boreal *Picea abies* forests (Taskinen et al. 2003). Soil respiration rates may also be directly linked to litter decomposition rates which were found to be reduced in gaps larger than 15 m diameter in subtropical forests in China (Zhang and Liang 1995, Zhang and Zak 1995). Thus the reduced gap soil respiration rates we observed may be due to both a reduction in fine root respiration and decomposition rates.

Reductions in carbon inputs into gaps may also result in reduced SOM. We observed a reduction in SOM in all gaps larger than 10 m but these reductions were not statistically significant. We did however find a significant reduction across all gap sizes in labile C, which is a subset of SOM, with the greatest differences in the 30 and 50 m gap sizes. Since the vast majority of SOM C is recalcitrant to decomposition, levels of labile C may be a more accurate indicator of more recent C input (Davidson et al. 1987, Parton et al. 1987). In his study of labile C pools in 30 m European beech forest gaps, Bauhus (1996) also reported reductions. These reductions were thought to be related to gap microclimate and reduced rooting.

Nitrogen Dynamics

Harvested forests tend to lose mineralized nitrogen at much higher rates than in undisturbed forests (Vitousek et al. 1979, Matson 1985, Bowden and Bormann 1986, Prescott et al. 2003,). This phenomenon has also been observed in temperate hardwood forest gaps (Bauhus and Bartch 1995, Bartsch 2000, Ritter et al. 2005b) and in tropical forest gaps (Denslow et al. 1998). The mineralized nitrogen that is not directly taken up by plants via their fine roots and mycorrhizal fungi can potentially be lost via denitrification or leaching. We use denitrification potential as a relative indicator of mineralized nitrogen availability to soil microorganisms (Griffiths and Swanson 2001). As in other disturbed forest systems, we predicted that denitrification potential would be higher in gaps than in surrounding forest soils. We found that denitrification potentials in gaps were roughly twice that found in the surrounding forest. In Brumme's (1995) study of beech forest gaps, N_2O emissions were 6 times higher in the center of 30 m gaps than in the surrounding forest. He speculated that this was due to the higher moisture levels found in gaps. It is also likely that this increase was also due to an increase in soil nitrate concentrations. In a study of nitrate concentrations in soil solutions within *Pinus contorta* stands of southeastern Wyoming, Parsons et al. (1994a) reported significant elevations in nitrate concentrations in gaps created when 15 to 30 trees were removed with the level of response directly related to gap size. Walters et al. (2006) reported finding increases of *in situ* net N mineralization in British Columbia cedar-hemlock gaps. Taken together, these results suggest that the network of fine roots and their associated fungi have been significantly disturbed as the result of gap formation. This results in the loss of mineralized N and labile C from gap soils and the reduction in soil respiration.

Soil Microflora

β-glucosidase levels are thought to act as a relative indicator of microbial activity (Skujins 1976). Levels found in this study are close to those observed more recently in forests and adjacent meadows in and near he H.J. Andrews Experimental Forest (Griffiths et al. 2005). These levels were significantly lower in both 50 m gaps than in adjacent forests. This reduction was essentially the same as that of *in situ* field respiration (about 24%). Significant reductions in microbial biomass have also been reported in three-year-old gaps in 100 year old Scots pine (*Pinus sylvestris*) organic

soils (Bååth et al. 1995) and microbial carbon was significantly reduced in organic soil layers in 2 year old gaps in boreal spruce (*Picea abies)* (Siira-Pietikäinen et al. 2001). Zhang and Zak (1998) also reported reduced fungal and bacterial biomass in large (15 to 50 m gaps) vs small (≤ 5 to 15 m) in subtropical forests. They also found a direct link between fungal biomass and plant litter decomposition rates.

Soil microbial C and N were determined in German beech forest gaps by Bauhus and Barthel (1995). They report a reduction of 21 and 22% for microbial C and N respectively in gap soils. It was speculated that this reduction was caused by a reduction in ectomycorrhizal fungal biomass. Ectomycorrhizal root tips were also found to decrease in the same gaps (Beon 1993) which might have been caused by new root growth being limited to 5 m from the edge two to three years after harvest (Bauhus and Bartsch 1996). Similar results have been reported by Parsons et al. (1994b) in their study of Wyoming lodgepole pine forests.

Based on our chronosequence study in the H. J. Andrews coniferous forests (Griffiths and Swanson 2001) we predicted mats would be greatly reduced in gaps even 9 years post harvest. We observed that there was a drastic reduction in both *Gautieria* and *Hysterangium* type mat coverage within both 50 m gaps. The gap size study yielded essentially the same conclusion. In gaps ranging from 10 to 50 m, coverage of mats was reduced to 5 % in gap soils compared to coverage of 15 to 20% in non gap soils.

The reduction in mycorrhizal mats observed in these gaps may partially explain elevated gap denitrification potentials. Bauhus and Barsch (1996) suggested that the reduction in gap fine-root biomass may result in nutrient losses. Cutting the dominant overstory trees during gap formation undoubtedly reduced active roots and their associated mycorrhizal fungi. The elevated denitrification potentials observed even 9 years after gap formation suggests that the belowground network of fine roots and mycorhhizal fungi that acted as an effective nitrogen sink was still not functioning as it would in mature forests because of reduced mat coverage in forest soils. As measured by mat coverages, the recovery of mycorrhizal mats may require more than 40 years before this network is back to where it was prior to harvest (Griffiths and Swanson 2001).

Conclusions

Contrary to our working hypothesis at the beginning of the study, there was no apparent connection between above ground gap coarse woody debris and vegetation biomass patterns and below ground soil characteristics. When comparing soils in gaps of varying sizes, not all soil characteristics responded to increasing size in the same way. Soil moisture increased and ectomycorrhizal mats were reduced in gaps of all sizes. In contrast, SOM and soil respiration were reduced only in gaps larger than 10 m diameter and litter depths were reduced the most in 50 m diameter gaps. Carbon inputs were reduced in larger gaps but mineralizable N increased. These data suggest that even after 5-9 yr of vegetation establishment, the effects of the overstory gap-creation harvest were still being reflected in forest soils.

The study illustrates that canopy gaps of different sizes can influence soil properties but that differences between gaps and non-gaps and gaps of different sizes will vary depending on the soil attribute. Although no evidence was found of fine-scale vegetation and coarse-woody debris influences on soils in these gaps, it could be that evidence of such influences would be found where patches of shrubs and large decayed tree boles had occupied microsites for many decades. The study further indicates that natural and silviculturally created gaps can influence forest soils but that the effects of the gaps are spatially variable and can be overridden by other factors such as pre-existing soil patterns and topography. Our results suggest that management with gap creation in these forests will modify nutrient cycling to some extent, and provide local hot-spots of nitrogen availability to plants and herbivores. Changes in ecosystem function will likely be ephemeral as tree roots and canopies reoccupy and dominate gaps.

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