

Soil Respiration and Carbon Responses to logging Debris and Competing Vegetation

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Management practices following forest harvesting that modify organic matter (OM) inputs and influence changes in the soil environment have the potential to alter soil C pools, but there is still much uncertainty regarding how these practices influence soil C flux. We examined the influence of varying amounts of logging-debris retention (0, 40, and 80% coverage) and vegetation control (initial or annual applications) on in situ bulk soil respiration, microbial respiration, and total soil C at two Douglas-fir [*Pseudotsuga menziesii* (Mirb.) Franco] sites. Annual vegetation control decreased bulk respiration, which was attributed to reduced root respiration and OM inputs when competing vegetation was absent. There was no difference in potential microbial respiration or total soil C pools between vegetation-control treatments, indicating that OM inputs from competing vegetation were rapidly consumed in situ. Logging-debris retention reduced bulk respiration, microbial respiration, and soil temperature, but the significance and magnitude of the difference were variable. A soil temperature function explained between 44 and 76% of the variation in microbial and bulk respiration, but there was no effect of reduced temperature on microbial respiration with 40% coverage. Total soil C at the end of the experiment was higher with 80% coverage at the site with relatively low initial total soil C, but there was also a significant increase in total soil C at both sites when the logging debris was removed. The results suggest that root decomposition following harvesting causes an increase in total soil C, which is dependent on the magnitude of logging-debris retention, its influence on the soil environment, and ultimately the microbial response.

Abbreviations: DOC, dissolved organic carbon; OM, organic matter; SOM, soil organic matter; SWC, soil water content.

Soil organic matter (SOM) is recognized as a critical soil property controlling soil productivity because of its beneficial effects on aeration, water holding capacity, and nutrient cycling, and it has been argued that a reduction in SOM (or soil C as a surrogate) has a high potential to reduce soil productivity in the long term (Jurgensen et al., 1997; Powers et al., 1990). Consequently, much effort has been spent examining the effect of forest harvest and management practices on SOM pools in intensively managed forests (e.g., Powers et al., 2005). More recently, interest in maintaining or enhancing SOM pools has been associated with the contribution of soil C efflux to atmospheric C following harvesting (Epron et al., 2006) and possible C sequestration in forest soils (Heath et al., 2003). Thus, there is great interest in maintaining or enhancing SOM pools in intensively managed forests.

Ecosystem C flux is dominated by soil respiration (hereafter referred to as *bulk respiration*) (Valentini et al., 2000), which arises from the respiration of living roots, microbial decomposition of root-derived C compounds in the rhizosphere (e.g., turnover and exudation), and microbial respiration during decomposition of SOM (Hanson et al., 2000). Changes in root and rhizosphere respiration following harvest have low potential to alter soil C stocks because this C source is largely external to the soil. In contrast, changes in microbial respiration could cause a concurrent change in SOM and total soil C. When soil C pools are in the so-called "steady state" commonly assumed for intact forests (Bowden et al., 1993; Davidson

Soil Sci. Soc. Am. J. 74:936–946

Published online 23 Feb. 2010

doi:10.2136/sssaj2009.0234

Received 24 June 2009.

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et al., 2002; Raich and Nadelhoffer, 1989), microbial respiration is balanced by OM inputs from above- and belowground litter. Harvesting alters the rate and relative source contribution to total litter input, generally decreasing aboveground inputs of fresh leaf litter, but root death from the harvested stand and logging residues may offset any aboveground reduction (Epron et al., 2006). Although the net change in litter input will vary with site conditions and harvest-related management practices, increased soil temperature and modified soil moisture following harvest are generally conducive to an increase in microbial respiration, possibly leading to an imbalance of the steady-state condition and a decline in soil C.

Management practices following harvest that promote OM inputs to the soil and reduce changes in the soil environment have the potential to mitigate changes in microbial respiration. The decision to remove (or retain) logging debris at the time of harvest is one practice likely to influence microbial respiration by those modes. Logging debris contains approximately 50% C by mass, and although a large portion of this C is respired to the atmosphere (Mattson et al., 1987; Palviainen et al., 2004), studies have shown significant inputs to the soil as dissolved organic C (DOC) and fine particulate OM (Mattson et al., 1987; Piirainen et al., 2002; Qualls et al., 2000; Robertson et al., 2000). Logging debris also shades the soil surface, generally causing a reduction in soil temperature (Devine and Harrington, 2007; Roberts et al., 2005), which would be expected to reduce rates of microbial respiration. Several long-term studies (>10 yr), however, have found no lasting effect of logging-debris retention on total soil C pools following harvest (Johnson et al., 2002; Olsson et al., 1996), including summary findings from 26 installations in the Long-Term Soil Productivity network that covered a wide range of site and climate conditions (Powers et al., 2005).

Given that at least some C in logging debris enters the soil, and disregarding any methodological bias, there are two possibilities for the above results. First, inputs from logging debris may be offset by an increased C efflux from the soil, via either increased microbial respiration or greater DOC leaching. Greater DOC loss following logging-debris retention is unlikely (Slesak et al., 2009), but microbial respiration could increase in response to increased substrate availability (Epron et al., 2006; Sulzman et al., 2005) or changes in the soil environment conducive to microbial activity such as an increase in pH (Belleau et al., 2006) or greater soil moisture (Rey et al., 2002). Second, spatial variability of soil chemical properties is high, resulting in a relatively large minimum detectable change for those properties following experimental manipulation (Homann et al., 2001; Rothe et al., 2002). Total soil C has also been shown to increase following harvest regardless of OM retention (Powers et al., 2005), and this increase may overwhelm any change associated with logging debris. It is possible that logging debris does modify soil C pools, but the magnitude of the change may be too small to be statistically identifiable in the presence of background variability.

Competing vegetation regrowth (i.e., non-crop species) may also mask or alter the effect of logging debris on microbial respi-

ration. In situ separation of the microbial respiration component of bulk respiration is difficult (see Hanson et al. [2000] for a review of methods), leading some investigators to measure bulk respiration as a surrogate for microbial respiration following harvest, assuming that the root contribution to bulk respiration is low (Hendrickson et al., 1989; Toland and Zak, 1994). Such an assumption may not be valid, as Edwards and Ross-Todd (1983) found greater in situ bulk respiration when logging debris was retained relative to removal treatments but observed the opposite response in lab incubations when the influence of vegetation (i.e., root respiration) was removed. Competing vegetation also has the potential to alter microbial respiration directly through additional modification of the soil environment (Gurlevik et al., 2004; Roberts et al., 2005), increased inputs of OM to both above- and belowground pools (Shan et al., 2001), and changes in microbial biomass and population structure (Busse et al., 2001; Li et al., 2004). A number of studies have documented a strong control of vegetation on bulk respiration in intact forests (Campbell et al., 2004; Hogberg et al., 2001), which appears to be largely driven by rates of photosynthesis (Hogberg et al., 2001; McDowell et al., 2004; Tanget al., 2005). Competing vegetation present following harvest could have as great or greater influence on bulk respiration than vegetation in an intact forest, overriding any modification to microbial respiration associated with logging-debris retention.

We examined the effect of logging-debris retention with initial or annual applications of vegetation control on in situ estimates of bulk and microbial respiration and soil C following clear-cut harvest at two sites that supported Douglas-fir forests in the Pacific Northwest to determine if the null effect of logging-debris retention on total soil C observed by other studies (e.g., Powers et al., 2005) applies to this region and whether or not changes in microbial respiration could account for any observed effect on total soil C. The specific objectives were to determine (i) the contribution of recently fixed C to bulk respiration when only initial vegetation control is applied, (ii) if varying amounts of logging-debris retention modify microbial respiration and how the relationship varies in the presence and absence of competing vegetation, (iii) the causal mechanisms for changes in microbial respiration and bulk respiration, and (iv) if changes in microbial respiration could explain any changes in total soil C. The effects of the treatments were examined at two sites that differ in soil properties and annual precipitation to determine if treatment responses were altered by those site variables.

MATERIALS AND METHODS

Site Characteristics

This study is part of a larger research project initiated at two sites in 2003 to assess the long-term effects of logging-debris retention and vegetation-control treatments on soil properties, nutrient cycling, and Douglas-fir growth. Potential productivity as indicated by site index is similar between sites, but large differences exist in precipitation and soil properties (Fig. 1; Table 1). The Matlock site is located on the Olympic Peninsula in the state of Washington, approximately 4 km southwest of

the town of Matlock. The soil at Matlock is classified as a sandy-skeletal, mixed, mesic Dystric Xerorthent, formed in glacial outwash with slopes ranging from 0 to 3% (Soil Survey Staff, 2005). The Molalla site is located approximately 24 km northeast of the town of Molalla, OR, in the foothills of the western Cascades. The soil at Molalla is classified as a fine-loamy, isotic, mesic Andic Dystrudept, formed in basic agglomerate residuum with slopes ranging from 2 to 40% (Soil Survey Staff, 2005). The regional climate is Mediterranean, characterized by mild, wet winters and dry, warm summers with periods of drought (2 mo) common. During the study period (2005–2007), the mean monthly air temperature at each site was similar among years, generally reaching the annual maximum in July (Fig. 1). Almost no rain occurred in July and August of 2006, but rain fell in every month of the 2007 growing season (Fig. 1).

Experimental Design and Treatment Application

The sites were initially clear-cut harvested with chainsaws and ground-based log removal in the spring of 2003. Log removal was limited to preassigned skid trails to isolate soil disturbance at each site. Following harvest, competing vegetation-control treatments (either initial or annual applications) were replicated eight times on 0.3-ha plots (50 by 60 m) in a randomized complete block design. All plots received an initial application of herbicide to reduce competing vegetation; at Molalla glyphosate [N-(phosphonomethyl)glycine] was aerially applied in August 2003, and triclopyr ([3,5,6-trichloro-2-pyridinyl) oxy]acetic acid) was applied with backpack sprayers at Matlock during September of 2003. Following this initial application, only those treatments assigned annual vegetation control were treated with herbicide in the spring. Both sites were planted with plug+ 1 bare-root Douglas-fir seedlings in February (Molalla) and March (Matlock) of 2004 at a 3- by 3-m spacing (1111 trees ha⁻¹). In March of 2005, three logging-debris treatments were applied to 2- by 2-m subplots centered on a single planted Douglas-fir within each 0.3-ha treatment plot. Woody logging debris was randomly applied to one of the subplots in each whole plot at a visually estimated surface coverage of 0, 40, or 80%. For each assigned treatment application, logging debris 5.0 to 12.5 cm in diameter was collected from buffer areas adjacent to the associated whole plot and added to the preexisting logging debris until the assigned coverage ($\pm 10\%$ with visual determination) was reached. In the case of the 0% treatment, all logging debris was removed from the subplot, but no attempt was made to remove legacy wood if present.

Debris volume was estimated with the line-transect method (Brown, 1974) and converted to a mass estimate (assumed wood density of 0.48 Mg m⁻³). The corresponding mass of logging debris in the 40 and 80% coverage was 13 (SD = 5.2) and 30 (SD = 8.5) Mg ha⁻¹, respectively, at Matlock, and 14 (SD = 5.2) and 29 (SD = 10.7) Mg ha⁻¹, respectively, at Molalla. The overall design is a randomized complete block with a split-plot arrangement of treatments: one whole-plot factor (vegetation control) and one subplot factor (logging-debris coverage).

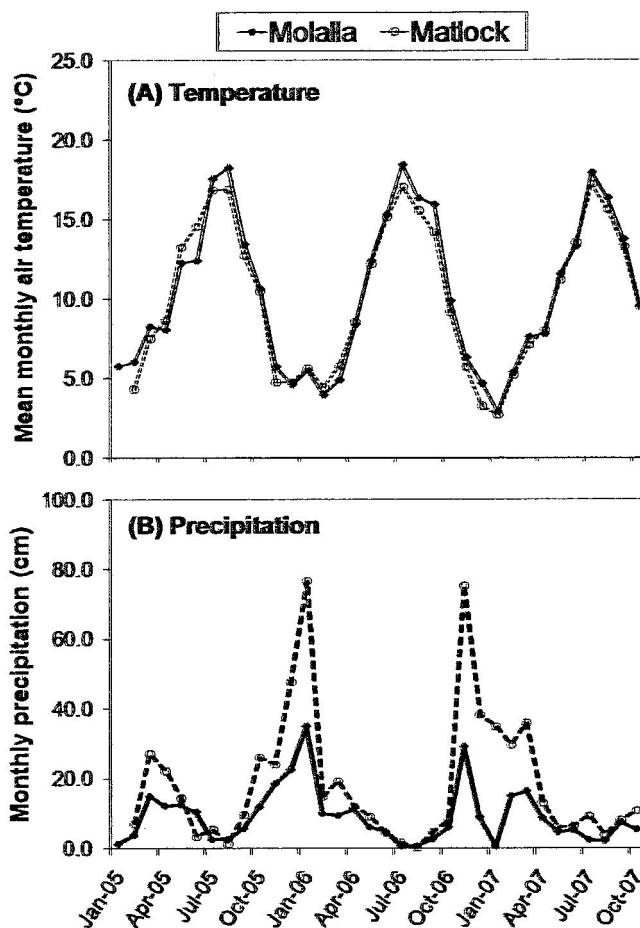


Fig. 1. Mean monthly (A) air temperature and (B) precipitation at Molalla and Matlock for the study duration.

Table 1. Site characteristics and selected pretreatment soil properties from samples collected to a depth of 30 cm for study sites near Molalla, OR and Matlock, WA.

Characteristic or property	Molalla	Matlock
Location	45.196° N, 122.285° W	47.206° N, 123.442° W
Elevation, m	449	118
Mean annual temperature, °C	11.2	10.7
Mean annual precipitation, cm†	160	240
50-yr site index, m‡	36	36
Particle size distribution§		
Sand, %	37	65
Silt, %	34	14
Clay, %	29	21
Bulk density, Mg m ⁻³ ¶	0.98 (0.02)#	1.45 (0.05)
Coarse fragments by mass, %	37.7 (2.2)	67.6 (1.3)
Total soil N, kg ha ⁻¹ ††	4338 (173)	2246 (88)
Total soil C, Mg ha ⁻¹	102.2 (4.7)	66.5 (3.6)

† Precipitation was estimated from the PRISM model for 1950–2005 (PRISM Climate Group, 2008).

‡ Harrington and Schoenholtz (2010).

§ Determined by the hydrometer method.

¶ Volumetric core sampler at Molalla, quantitative pits at Matlock (Meehan, 2006).

Standard error in parentheses, $n = 8$ for bulk density at Matlock, $n = 24$ for all others.

†† C and N concentrations of fine fraction (FF) determined by dry combustion on a CNS total analyzer; mass estimate calculated as the product of FF concentration and FF bulk density.

In Situ Soil Respiration and Associated Measures

At each subplot and at four locations within adjacent uncut reference forest, which served as an experimental control, two 15.25-cm polyvinyl chloride respiration collars were permanently installed at 3- and 30-cm depths in June 2005. The 3-cm collar was used to estimate bulk soil respiration, and the 30-cm collar was used to estimate microbial respiration by the root exclusion method (Hanson et al., 2000). Several studies have determined reasonable estimates of bulk and microbial respiration with the use of cores similar to those used in our study (Dilustro et al., 2005; Kelting et al., 1998; Vogel and Valentine, 2005). Respiration measurements were delayed for 3 mo following installation to reduce artifacts associated with increased heterotrophic decomposition of severed roots (Kelting et al., 1998). Root in-growth occurred in most of the collars to some extent by the end of the study period, with in-growth being much greater in the initial vegetation-control treatment relative to the annual vegetation-control treatment. There was little difference in root in-growth among logging-debris treatments within each herbicide treatment, and there was no detectable relationship between root in-growth biomass and estimates of microbial respiration (Slesak, 2008).

Beginning in September of 2005, bulk and microbial respiration were estimated on a monthly basis by measuring CO_2 efflux from each of the soil collars with the use of a portable infrared gas analyzer (LI-6250 LI-COR Biosciences, Lincoln, NE) attached to a custom-built closed dynamic soil respiration chamber. At the beginning of each measurement, CO_2 concentrations were scrubbed to approximately 10 uLL^{-1} below ambient, and then allowed to rise during measurement. Carbon dioxide concentration was recorded during a 5 uLL^{-1} change in chamber concentration at each of three consecutive measurements. The three measurements were averaged and used to calculate a mean estimate of CO_2 flux ($\text{umol m}^{-2}\text{s}^{-1}$) per collar and tree for each time period. All collars at a given site were measured during an approximate 6-h period (1000-1600 h) in a single day, and the other site was generally measured in the same manner on the following day for any monthly measurement period. After each measurement, the soil temperature was measured to a depth of 10 cm with a temperature probe. The volumetric soil water content (SWC) was measured at 2-h intervals from a depth spanning 20 to 40 cm in each subplot with ECH_2O probes (Decagon Devices, Pullman, WA). The mean SWC on the day of measurement was used for all analyses in this study.

Laboratory Incubations for Microbial Respiration

Soil samples were collected from half of the subplot replications ($n = 4$ for each vegetation-control and logging-debris subplot combination at each site) in April, June, and September of 2006 and in June of 2007 to measure potential microbial respiration under controlled temperature and moisture conditions in the laboratory. Mineral soil was collected to a depth of 20 cm at three random locations in each subplot and composited. Before sampling, the forest floor was removed from the soil surface to ensure that only the mineral soil was collected for analysis. The soil morphology was relatively uniform within the 20-cm sample depth, which corresponded with the A horizon of the soil profile at each site. The samples were air dried, passed through a 2-mm sieve, and then stored at 4°C before analysis.

For each sample collection period, approximately 50 g of air-dried, sieved soil was incubated in a microlysimeter constructed of benchtop filtration units (Falcon Filter, Becton Dickinson Labware, Franklin Lakes, NJ) as described by Nadelhoffer (1990). Samples were incubated in the microlysimeters for 17 d at 25°C and a soilwater potential of -22 kPa . Microbial respiration was estimated by measuring the CO_2 evolution at Days 3, 10, and 17 of the incubation period. At each measurement, the microlysimeters were allowed to incubate for approximately 1.5 h, and then the headspace gas was analyzed for CO_2 concentration on a gas chromatograph (5700 A series, Hewlett-Packard). The headspace volume, air pressure and temperature, and soil mass were used to convert CO_2 evolution to an estimate of CO_2 flux ($\text{mg C kg}^{-1} \text{ soil h}^{-1}$). The three measures for each unit were averaged to determine a mean soil respiration rate for each replication at each incubation period.

Mineral Soil Carbon

Soil samples were collected from each subplot replication in July 2005 and October 2007 to assess treatment effects on the total soil C concentration during the study period. Mineral soil was collected to a depth of 20 cm as described above. Samples were air dried and sieved to pass a 2-mm mesh, followed by grinding of a subsample to pass a 0.25-mm mesh. Ground subsamples were dried at 65°C for 1 d and then dry combusted on a Fisons NA1500 NCS Elemental Analyzer (ThermoQuest Italia, Milan, Italy) to determine the total soil C concentration. We did not assess the treatment effects on soil bulk density, but a related assessment conducted in 2005 found no distinguishable difference between pre- and post-treatment estimates of bulk density at the 0- to 15-cm depth and no differences between "light" and "heavy" logging-debris coverage or between vegetation-control treatments (S. Gall. unpublished data, 2005).

Data Analysis

A mixed model with repeated measures was used to assess treatment effects on bulk respiration, soil temperature, and soil moisture. Both block and block $\times$ whole-plot factor interactions were modeled as random effects, with the whole-plot factor, subplot factor, and month modeled as fixed effects. The effect of vegetation control on microbial respiration measured in situ was not assessed given the systematic bias associated with greater root in-growth in the initial vegetation-control treatment (Slesak, 2008), but the relative effect of logging-debris coverage on in situ microbial respiration was assessed for each herbicide treatment independently. Statistical analysis of in situ data was limited to growing-season months (defined here as April-September) in each year to identify appropriate covariance matrices for repeated measures analysis while focusing on the time period when treatment effects were expected to be greatest. Logarithmic transformation was necessary to meet assumptions of normality and heterogeneity for the respiration variables. A priori orthogonal contrasts were performed to test for a significance of difference between (i) the absence and presence of debris (0% coverage vs. the mean of the 40 and 80% coverage treatments), and (ii) the 40 and 80% logging-debris coverage treatments. Tukey's honestly significant difference test was used to determine significant differences among least-squares means for the incubation and soil C data, while

t-tests were used to determine if the change in soil C within a treatment during the study period was significantly different from zero.

The dependence of soil respiration on soil temperature was assessed with the following exponential function as described by Lloyd and Taylor (1994);

$$CO_2 = \beta_0 \exp(\beta_1 T) \quad [1]$$

where CO_2 is the estimated flux of CO_2 (in $\mu\text{mol m}^{-2} \text{s}^{-1}$), B_0 and B_1 are fitted parameters, and T is the temperature (in $^{\circ}\text{C}$). The parameter B_0 is the basal rate of respiration at 0°C , which has been interpreted as an indication of C quality (Fierer et al., 2005). Note that the exponential temperature coefficient B_1 is related to the Q_{10} value where $Q_{10} = e^{B_1 \cdot 10}$. Nonhomogenous variance required logarithmic transformation of the temperature function for proper parameter estimation. For each growing season (6-mo period), a comparison of the regression lines was performed to determine if the parameters differed by treatment. The data were fit to alternative models that tested for (i) different intercepts, (ii) different slopes, (iii) both different intercepts and slope, and (iv) no difference among treatments. Parameters were back-transformed when necessary (i.e., B_0 when regression lines were compared) for interpretation. An α level of 0.05 was used to assess statistical significance in all evaluations. All analyses were performed in SAS Version 9.1 (SAS Institute, Cary, NC).

RESULTS

Vegetation-Control Effects

During the 2-yr study period, the median bulk respiration ranged from 0.52 to $5.45 \mu\text{mol m}^{-2} \text{s}^{-1}$ at Molalla and from 0.58 to $4.65 \mu\text{mol m}^{-2} \text{s}^{-1}$ at Matlock, with a seasonal trend positively related to soil temperature (Fig. 2). Bulk soil respiration in the reference forest showed notable similarity with that in the initial vegetation-control treatment but not the annual vegetation-control treatment. Bulk respiration decreased following annual vegetation control at both sites in some months of the growing season during each year, with the greatest duration and magnitude of the effect occurring at Molalla (Table 2). The soil temperature increased by approximately 0.8°C (range 0.6 – 1.1°C) when annual vegetation control was applied at Molalla during some months of the growing season, but there was no discernable effect at Matlock. The soil water content increased following annual vegetation control at both sites in

2006 and at Molalla in 2007, but the magnitude of the effect varied by month. Increases in SWC in the annual vegetation-control treatment at Molalla ranged from 0.08 to 0.11 and 0.05 to $0.08 \text{ m}^3 \text{ m}^{-3}$ in 2006 and 2007, respectively, and increases in SWC with annual vegetation control at Matlock ranged from 0.05 to $0.10 \text{ m}^3 \text{ m}^{-3}$ in 2006.

At Molalla, bulk respiration in the initial vegetation-control treatment was greatest before the peak soil temperature in each year, but bulk respiration in the annual vegetation-control treatment occurred at or following the peak soil temperature (Fig. 2). The earlier reduction in bulk respiration in the initial vegetation-control treatment occurred in both years when SWC was $<0.21 \text{ m}^3 \text{ m}^{-3}$, suggesting a water limitation to bulk respiration below this value. Water limitation to bulk respiration was also evident at Matlock, where the minimum bulk respiration in 2006 coincided with the minimum SWC in August, followed by an increase in bulk respiration in September when the SWC increased and soil temperatures were still relatively warm. In 2007 when rainfall extended into the growing season (Fig. 1), a higher SWC was associated with higher bulk respiration at both sites. At Molalla, the effect was limited to the initial vegetation-control treatment, but at Matlock, both vegetation-control treatments had greater median bulk respiration in 2007 than 2006.

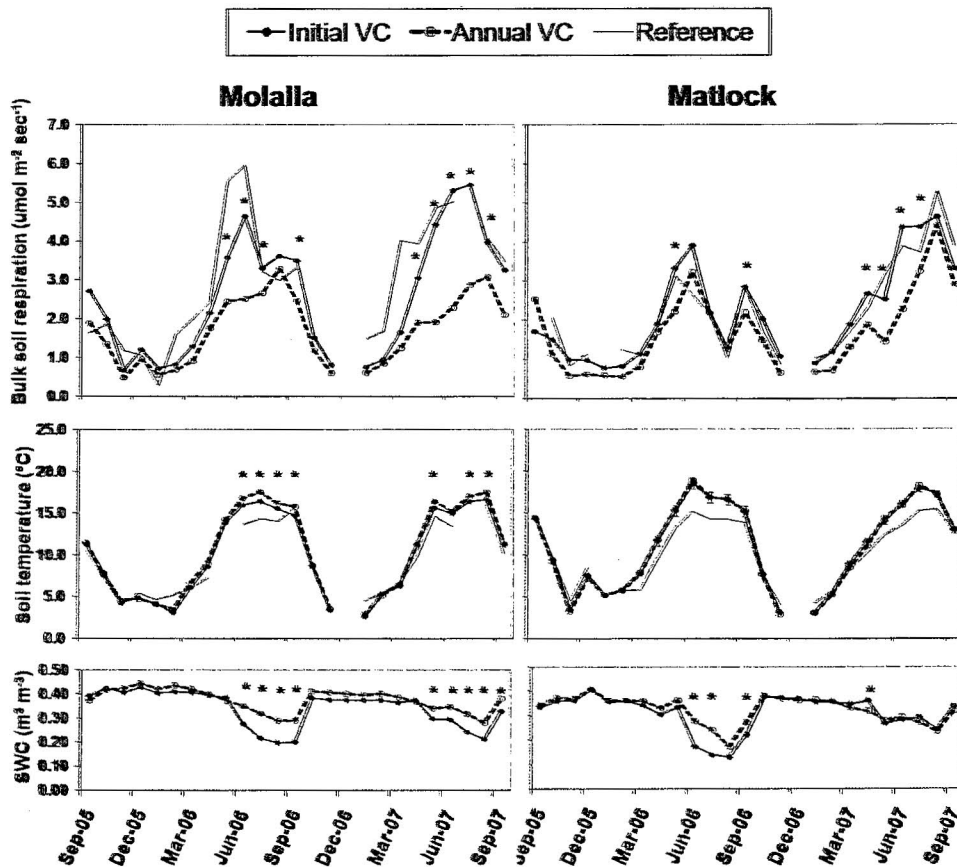


Fig. 2. Bulk soil respiration, soil temperature, and volumetric soil water content (SWC) by sample month and competing vegetation control (VC) treatment at Molalla and Matlock. *Significant difference between treatments for the associated month. Only data from April to September in each year were analyzed.

Table 2. The *F* statistic Probabilities from ANOVA by year for the dependent variables, soil water content, soil temperature, and bulk soil respiration at Molalla and Matlock.

Effects	Molalla			Matlock		
	Soil water content	Soil temp.	Bulk soil respiration	Soil water content	Soil temp.	Bulk soil respiration
2006						
Vegetation control (VC)	0.017	0.002	0.005	0.006	0.769	0.156
Debris (D)	0.141	<0.001	0.003	0.367	<0.001	0.355
VC × D	0.568	0.099	0.818	0.468	0.462	0.501
Month (M)	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001
VC × M	<0.001	<0.001	<0.001	0.002	0.463	<0.001
D × M	0.700	<0.001	0.008	0.804	<0.001	0.194
VC × D × M	0.238	0.690	0.666	0.297	0.959	0.241
2007						
VC	0.041	0.018	0.003	0.360	0.868	0.009
D	0.423	<0.001	0.112	0.023	<0.001	0.591
VC × D	0.768	0.096	0.545	0.101	0.817	0.634
M	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001
VC × M	<0.001	<0.001	<0.001	0.080	0.020	<0.001
D × M	0.986	<0.001	0.652	0.534	<0.001	0.579
VC × D × M	0.757	0.028	0.942	0.171	0.838	0.337

Logging-Debris Effects

Bulk respiration followed a general pattern of decreasing flux with increasing logging-debris coverage at both sites, but differences among treatments were only Significant at Molalla during the 2006 growing season (Fig. 3). During that year, the contrast

Examination of the microbial respiration data by vegetation-control treatment indicated similar effects of logging debris on microbial respiration as those observed for bulk respiration, but the magnitude and significance of the effects generally decreased due partly to a reduction in statistical power resulting from the

analytical approach necessitated by root in-growth. At Molalla, there was no effect of logging-debris coverage on microbial respiration in the initial vegetation-control treatment in either year ($P > 0.2$), but there was a significant effect ($P < 0.01$) in both years when annual vegetation control was applied (Fig. 4). At Matlock, significant effects were limited to 2006 when the 0% coverage had greater microbial respiration than both the 40 and 80% coverage in the initial vegetation-control treatment during September, and the 40% coverage had significantly greater microbial respiration than the 80% coverage in August.

Temperature Dependence of Soil Respiration

The temperature was significantly related to bulk and microbial respiration at each site in both years of the study, explaining between 40 and 75% of the variation in response (Table 3). At both sites and in both years, the intercept (B_0) for the log-transformed function was greater

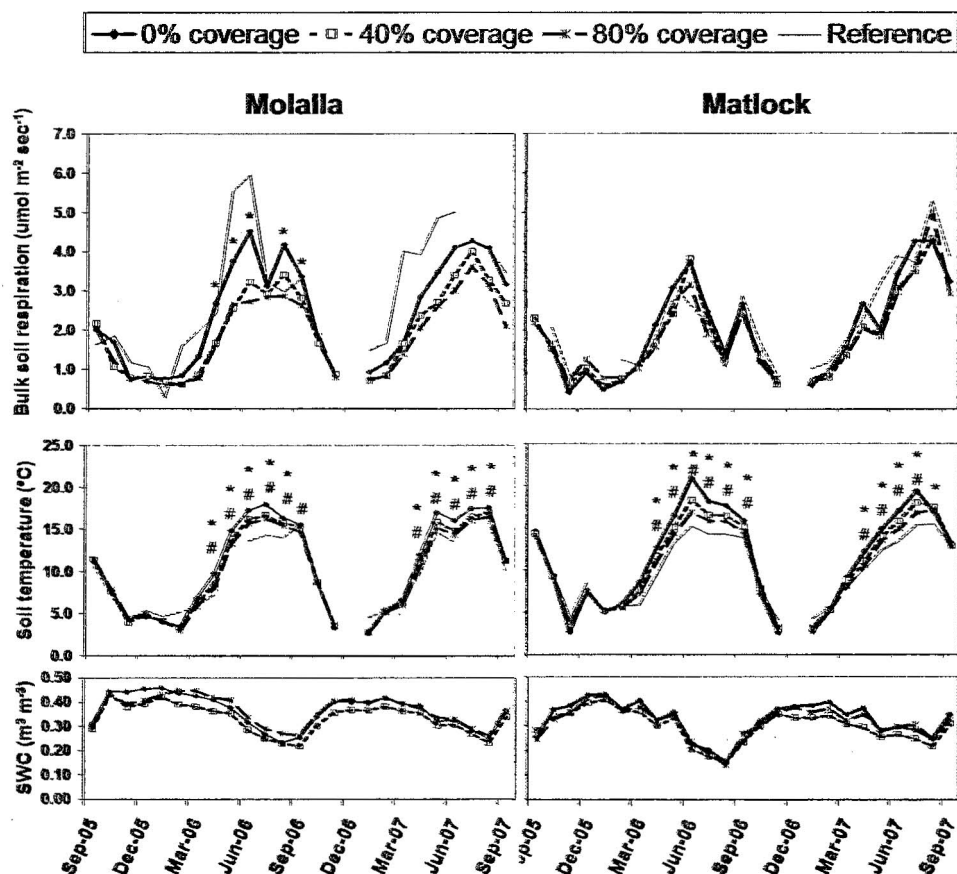


Fig. 3. Bulk soil respiration, soil temperature, and volumetric soil water content (SWC) by sample month and logging-debris treatment at Molalla and Matlock. *Significant contrasts between the absence and presence of logging debris. #Between 40 and 80% logging-debris coverage. Only data from April to September in each year were analyzed.

in the initial vegetation-control treatment than in the annual vegetation-control treatment. Molalla had back-transformed intercepts that were 0.49 and 1.40 $\mu\text{mol m}^{-2} \text{s}^{-1}$ higher in the initial vegetation-control treatment for the 2006 and 2007 growing seasons, respectively, compared with Matlock, which had back-transformed intercepts that were 0.31 and 0.66 $\mu\text{mol m}^{-2} \text{s}^{-1}$ higher with initial vegetation control in the same years. At Molalla, the temperature coefficient (B_1) was also significantly higher in the initial vegetation-control treatment in 2006 (0.093 and 0.062 for the initial and annual vegetation-control treatments, respectively). There were no differences in model parameters among logging-debris treatments at Matlock for either bulk or microbial respiration in either year. At Molalla, the model for 0% coverage had a greater intercept (B_0) than that for the 80% coverage for bulk respiration (back-transformed increases of 0.60 and 0.58 $\mu\text{mol m}^{-2} \text{s}^{-1}$ for 2006 and 2007, respectively), and a significantly greater intercept than the model for the 40% coverage in 2006 (0.49 $\mu\text{mol m}^{-2} \text{s}^{-1}$ higher). Similar results were found when the microbial respiration data were fit to the model in 2006 (0% coverage with back-transformed intercept 0.41 $\mu\text{mol m}^{-2} \text{s}^{-1}$ greater than 80% coverage) (data not shown).

Microbial Respiration from Incubations

There was a significant effect of logging debris on microbial respiration at Molalla in the June 2006 incubation ($P = 0.045$), where 0% coverage had a microbial respiration rate that was approximately 20% (0.8 mg C kg⁻¹ soil h⁻¹) greater than either the 40 or 80% coverages (data not shown). There were no differences between vegetation-control treatments at either site for any incubation period. Mean microbial respiration in the June 2007 incubation (across all treatments) was approximately 40 and 30% lower than the June 2006 incubation at Matlock and Molalla, respectively.

Total Soil Carbon

There was no difference ($P > 0.2$) in total soil C concentration between vegetation-control treatments at either site in 2005 or 2007 (data not shown). Mean

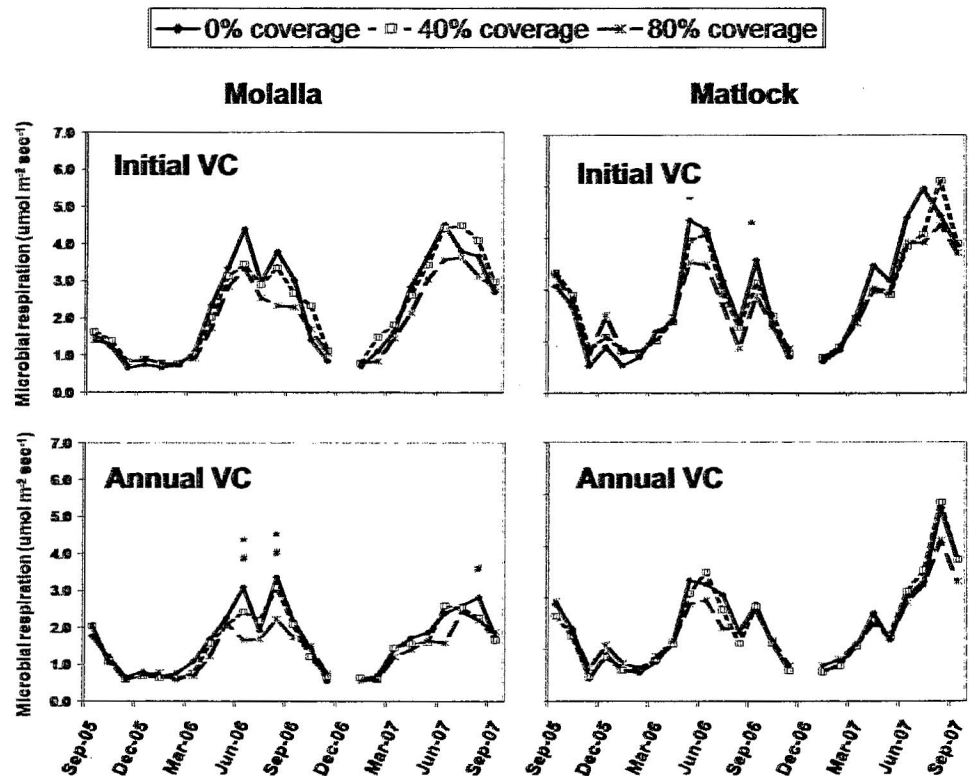


Fig. 4. Microbial soil respiration by sample month and logging-debris treatment with either initial or annual vegetation control (VC) at Molalla and Matlock. *Significant contrasts between the absence and presence of logging debris. #Between 40 and 80% logging-debris coverage. Only data from April to September in each year were analyzed.

total soil C concentrations tended to be greater in the 80% logging-debris treatment compared with the other treatments at both sites, but differences were only significant at Matlock ($P = 0.026$), where the 80% coverage had 14.8 g C kg⁻¹ (95% CI of 2.2–27.4) and 15.6 g C kg⁻¹ (95% CI of 3.6–27.6) greater total soil C concentration than either the 0 or 40% coverages, respectively (Fig. 5). Patterns in total soil C concentration change during the study period were similar between sites. From 2005 to 2007, total soil C concentration significantly increased in the 0% coverage, with a mean increase of 9.5 (95% CI of 0.6–18.4)

Table 3. Estimated fitted parameters β_0 and β_1 and coefficients of determination for the log-transformed soil temperature function for bulk soil and microbial respiration by vegetation-control (VC) treatment and year at Molalla and Matlock.

Treatment	Molalla			Matlock		
	log β_0	β_1	R^2	log β_0	β_1	R^2
<u>2006</u>						
Bulk soil respiration						
Initial VC	-0.57 (0.06)†	0.123 (0.005)	0.57	-0.48 (0.07)	0.083 (0.006)	0.45
Annual VC	-0.91 (0.05)	0.120 (0.005)	0.69	-0.83 (0.06)	0.094 (0.005)	0.52
Microbial respiration						
Annual VC	-0.70 (0.05)	0.095 (0.004)	0.64	-0.80 (0.05)	0.083 (0.004)	0.56
<u>2007</u>						
Bulk soil respiration						
Initial VC	-0.28 (0.07)	0.118 (0.006)	0.67	-0.54 (0.05)	0.117 (0.004)	0.76
Annual VC	-0.58 (0.07)	0.096 (0.006)	0.55	-0.70 (0.06)	0.106 (0.005)	0.44
Microbial respiration						
Annual VC	-0.64 (0.06)	0.089 (0.005)	0.58	-0.71 (0.05)	0.095 (0.004)	0.65

† Standard error in parentheses.

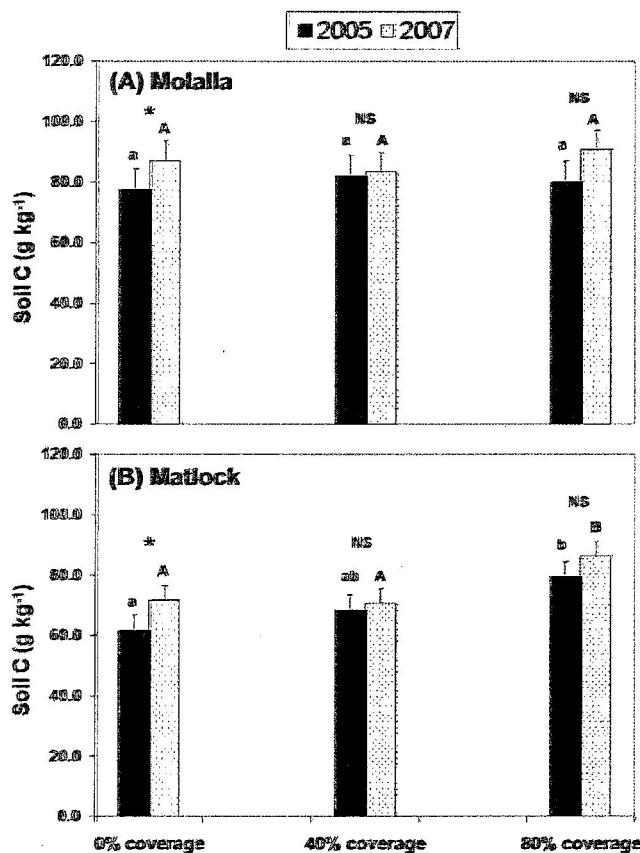


Fig. 5. Total soil C concentration to a depth of 20 cm by sample period and logging-debris treatment at (A) Molalla and (B) Matlock. Means within a year followed by a different letter (lowercase letters for 2005 and uppercase letters for 2007) are significantly different ($P \leq 0.05$). *Significant ($P \leq 0.05$) differences between the two measurement periods; NS, no significant difference between periods. Error bars are standard error of the mean.

and 10.1 (95% CI of 0.3-19.8) gC kg^{-1} at Molalla and Matlock, respectively. There was little change in total soil C concentration during the study period in the 40% coverage treatment, but the mean total soil C concentration tended to be higher in 2007 than in 2005 at both sites in the 80% coverage treatment.

DISCUSSION

Vegetation-Control Effects

There is a potential for annual applications of vegetation control to reduce soil C pools (Miller et al., 2006; Echeverria et al., 2004), but our results suggest that the likelihood of such an outcome is low at these study sites. No difference in potential microbial respiration (laboratory determined) between vegetation-control treatments indicated that OM inputs from competing vegetation were rapidly consumed in situ. Higher soil temperature with annual vegetation control at Molalla probably resulted in greater rates of in situ microbial respiration, but the amount would have been small based on the estimated parameters in Table 3 and the mean monthly temperatures from each treatment (accounting for, at most, 10 and 5% of bulk respiration in 2006 and 2007, respectively). The above, in addition to no difference in the total soil C concentration after 4 yr of treatment application (vegetation-control treatments began in 2003) indi-

cates small potential for a reduction in SOM pools when annual vegetation control is used. McFarlane et al. (2009) also found no effect of annual vegetation control on total soil C in ponderosa pine (*Pinus ponderosa* P. Lawson & C. Lawson) plantations across a productivity and mineral soil C gradient ($15\text{--}50 \text{ gC kg}^{-1}$) in northern California.

Soil respiration in an intact forest is dominated by sources of recently fixed C (e.g., root metabolism, leaf litter, and root turnover) (Trumbore, 2000; Giardina et al., 2004), and this appears to be the case following harvest at these sites given the above results. Studies that have measured bulk respiration following harvest have commonly assumed that the contribution of root respiration and recently fixed litter to bulk respiration is small (e.g., Toland and Zak, 1994; Hendrickson et al., 1989; Londo et al., 1999) and have concluded that increased or similar bulk respiration relative to uncut forest is indicative of greater SOM decomposition in harvested areas. In this study, estimated rates of bulk respiration in the initial vegetation-control treatment and reference forest were comparable at each site, but bulk respiration in the annual vegetation-control treatment was lower than the reference forest in most months of the growing season. Although the relative source contribution to greater bulk respiration in the initial vegetation-control treatment is uncertain, it is clear that the increase arose primarily from sources of recently fixed C (i.e., fixed post-harvest). The relative increase in bulk respiration that can be attributed to recently fixed C (calculated as the difference between treatments in bulk respiration relative to the annual vegetation-control treatment) during the growing season was, on average, 49% (range 24-85%) and 89% (range 29-133%) at Molalla in 2006 and 2007, respectively, and 39% (range 29-49%) and 61% (range 35-92%) at Matlock for the same years. These estimates are fairly conservative, as they do not account for root respiration from Douglas-fir trees in the annual vegetation-control treatment. Clearly, sources of recently fixed C can contribute a substantial amount to bulk respiration in the initial years following forest harvest, indicating that the assumption of bulk respiration dominated by microbial respiration following harvest is not valid in all situations.

logging-Debris Effects

Although there were few significant differences in microbial respiration among the logging-debris treatments, the general patterns that were observed suggest that microbial respiration was modified by the logging debris. At both sites, microbial respiration in the 80% coverage treatment was consistently lower than in the 0% coverage treatment during most months of the growing season in each year, but microbial respiration in the 40% coverage treatment was similar to or exceeded that in the 0% treatment. Bulk soil respiration showed a similar pattern, which probably reflects differences in microbial respiration as well. It appears that high amounts (i.e., 80% coverage) of logging-debris retention reduce microbial respiration at these sites, but moderate amounts have little effect or potentially a positive effect on microbial respiration.

Given the strong temperature dependence of soil respiration observed here and in other studies (e.g., Lloyd and Taylor, 1994, and references therein), it is probable that lower microbial respiration and bulk respiration in the 80% coverage treatment was primarily due to reductions in soil temperature that occurred with this treatment. Other factors probably contributed to the difference at Molalla in 2006, however, given that the potential microbial respiration determined in the July incubation and the intercept of the temperature function were significantly higher in the 0% coverage treatment. During that year, higher soil temperature in the 0% coverage treatment probably increased residual (from the previous stand) root decomposition (Chen et al., 2000), causing an increase in the amount of partially decomposed root material during the incubation (i.e., small enough to pass a 2-mm sieve) and a subsequent increase in potential respiration. The lack of a comparable effect in 2007 may indicate depletion of easily decomposable root C in the 0% coverage treatment, or the smaller differences in temperature among treatments that year may have dampened differences in root decomposition (Chen et al., 2000).

The absence of a microbial respiration response to the temperature decrease in the 40% coverage treatment may be associated with changes in the soil environment and its effect on microbial activity. In a related assessment, phospholipid fatty acid analysis indicated no difference in the microbial community structure among treatments, but a stress indicator (19:0cy/18:1w7c) was significantly lower in the 40% coverage treatment than the 0 and 80% treatments at both sites (Slesak, 2008). Stress indicators have been shown to increase following exposure to various environmental stresses including low pH, low moisture, and reduced O₂ availability (Petersen et al., 2002). More favorable environmental conditions could be associated with higher soil pH in the 40% coverage treatment (Slesak, 2008), differences in SWC, which was consistently lower in the 40% coverage treatment than either the 0 or 80% treatments at both sites (Fig. 4) (e.g., greater O₂ diffusion with lower SWC), or some other factor not assessed in this study. Although the mechanism is uncertain, it appears that reduced microbial stress resulted in greater microbial activity than would be predicted from temperature alone.

Differences in total soil C concentration at the end of the experiment generally agree with the microbial respiration results. The total soil C concentration was significantly higher in the 80% coverage treatment at Matlock, but there was little difference between the 0 and 40% coverage treatments, which would be expected given the similar microbial respiration rates between those treatments. The similar pattern observed at Molalla suggests the same mechanism, but differences may not have been detectable due to the greater soil C pool at that site. It appears that there is an effect of logging debris on the total soil C pools at these sites, but the effect is limited to situations where relatively large amounts of debris are retained and are undetectable when the initial soil C pool is large. In operational settings or experimental designs where treatments are applied to large areas, the effect of logging debris would probably be masked because

coverage is discontinuous and each of the debris treatments used in this study would be present to some extent regardless of the experimental treatment or operational practice (Meehan, 2006; Eisenbies et al., 2005).

Given the magnitude of increase in soil C in the 80% coverage at Matlock, much of the accumulation can be attributed to sources within the soil rather than inputs at the surface. Using the bulk density values in Table 1 (corrected for coarse-fragment content), the 14.8 g C kg⁻¹ increase in concentration corresponds to a C mass of 13.9 Mg C ha⁻¹, almost the same mass of C applied as logging debris (assuming a C concentration of 500 g kg⁻¹). Much of the logging debris still remains at the soil surface (R. Slesak, personal observation, 2008), and most C (>75%, Mattson et al., 1987) in logging debris is respired directly to the atmosphere, making it probable that C inputs from logging debris were a small contributor to the estimated 13.9 Mg C ha⁻¹ increase. The significant increase in soil C in the 0% coverage treatment at both sites, combined with greater microbial respiration, underscores the role of below ground decomposition in changes in soil C following harvest (Powers et al., 2005). Fine root decomposition could have contributed approximately 5 Mg ha⁻¹ C to any increase (assuming a relative fine root biomass of 10 Mg ha⁻¹ [Vogt et al., 1987] and a C concentration of 5 g kg⁻¹), indicating that some of the increase must have been derived from the forest floor or coarse root biomass, which can be as much as an order of magnitude greater than fine roots (McDowell et al., 2001).

Although differences in soil C may not be apparent, a relative mass balance calculation including DOC flux (Slesak et al., 2009) indicated that C lost from the mineral soil in the 0% coverage treatment was greater than the 80% coverage treatment, implying greater total belowground C (mineral soil + root necromass) in the 80% coverage treatment. Greater belowground C may have implications for soil C sequestration, but the stability of the fraction contributing to the increase (i.e., root necromass) could be low, resulting in no difference between logging-debris treatments during the course of a rotation. Further work is warranted to determine the stability of the observed increase in total soil C at these sites and to quantify any differences in belowground OM storage following logging-debris retention or removal.

CONCLUSIONS

Although annual vegetation control has the potential to reduce total soil C through a reduction in litter inputs, our results suggest a concurrent reduction in microbial respiration when litter inputs are reduced and a net result of no change in soil C beyond that which occurs following harvest. Much of the bulk soil respiration when only an initial vegetation control was applied was attributed to sources of recently fixed C, which conflicts with the common assumption of microbial-dominated soil respiration following forest harvest. High amounts of logging-debris retention reduced microbial respiration, probably due to a decrease in soil temperature and a subsequent reduction in belowground OM decomposition. In contrast, moderate amounts of logging debris had little effect on net microbial

respiration despite a reduction in soil temperature, suggesting that other factors may have as strong a control as soil temperature on soil respiration following harvest. Greater total soil C at one of the sites when high amounts of logging debris were retained indicates a beneficial effect on soil C pools, with the effect due to modification of the soil environment and its influence on belowground OM decomposition rather than an increase in C inputs to the soil. Logging debris retention may increase the total soil C in some situations, but the effect may not be apparent in the presence of the large concurrent increases in total soil C that occur following harvest.

ACKNOWLEDGMENTS

This is a product of the Sustainable Forestry component of Agenda 2020, a joint effort of USDA Forest Service Research and Development and the American Forest and Paper Association. Funds were provided by the Pacific Northwest Research Station. Research partners included Green Diamond Resource Company, Port Blakely Tree Farms LLC, Oregon State University, and Virginia Tech.

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