Forest soil respiration and exoenzyme activity in western North America following thinning, residue removal for biofuel production, and compensatory soil amendments

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Abstract
Cellulosic biofuel from forest thinning operations is a potential renewable energy source in regions with overstocked forests such as those in western United States. However, it is possible that biomass removal can deplete nutrients from soil, which can alter soil respiration ($R_s$) and exoenzyme properties, and potentially impact tree growth. This study evaluates the impact of biomass removal on $R_s$ and exoenzyme properties and the capacity of soil amendments to counteract any potential effects. At two study locations, we created four post-thinning biomass retention levels: full biomass removal (0×), full biomass retention (1×), double biomass retention (2×), and a no-thin treatment. Four soil amendment treatments were applied to each biomass retention level: N fertilizer (F), biochar (B), fertilizer plus biochar (FB), and an untreated control (C). We evaluated treatment effects on $R_s$ and activity of four exoenzymes to represent C-cycling, N-release, and P-release processes. Biomass retention levels had no effect on $R_s$ ($p = .42$) or exoenzyme activities ($p > .29$). Variation in exoenzyme activity was explained by location, season, soil organic matter, soil moisture content, and temperature. Variation in $R_s$ was explained by the same variables, in addition to C-cycling exoenzyme activity and soil pH. Soil amendments had no effect on exoenzyme activities ($p > .49$), and no main effect on $R_s$ ($p = .48$), though amendments influenced $R_s$ differently at each location ($p = .02$). Short-term findings suggest small-diameter biomass removal for cellulosic biofuel production will not impact $R_s$ and exoenzyme properties, and paired with our tree growth study, provide evidence that biofuel systems are a feasible renewable energy source in the western North America.

KEYWORDS
biochar, bioenergy feedstock, biomass removal, cellulosic biofuel, exoenzyme activity, nitrogen fertilizer, slash loading, soil respiration

1 | INTRODUCTION

Precommercial thinning is used to reduce tree competition and improve availability for resources such as light, water, and soil nutrients (Brockley, 2005; Chase, Kimsey, Shaw, & Coleman, 2016). The forests in western United States are estimated to be overstocked by 1.8 billion oven-dry metric tons of woody biomass that could be used for bioenergy
feedstock (Rummer et al., 2005). Removing the residues from thinning operations for use as a biofuel source can provide revenue that can mediate the cost of thinning, while also reducing the risk of wildfire and disease (Evans & Finkral, 2009; Schroeder, 2008). However, we have limited knowledge of how thinning residue removal operations will impact soil respiration ($R_s$) and exoenzyme properties such as biomass decomposition, soil nutrient cycling, and long-term forest productivity.

The impacts on soil properties from clear-cut harvests have been studied more than precommercial thinning impacts. Whole-tree biomass removal during clear cutting can lower soil nutrient availability (Johnson & Todd, 1998; Saarsalmi, Tamminen, Kukkola, & Hautajärvi, 2010), or have no impact on soil nutrients and site productivity (Slesak, Palik, D’Amato, & Kurth, 2017; Voldseth, Palik, & Elioff, 2011). Clear cutting shifts soil microbial function from nutrient limited and ectomycorrhizal dominated toward carbon limited and saprope dominated (Kyaschenko, Clemmensen, Hagenbo, Karltn, & Lindahl, 2017). Yet with thinning, soil microbial shifts are less definitive (Adamczyk, Adamczyk, Kukkola, Tamminen, & Smolander, 2015), which supports the idea that small-diameter biomass removal from precommercial thinning will likely impact site conditions less than clear-cut harvesting (Kabrick, Dwyer, Shifley, & O’Neil, 2013; Klockow, D’Amato, & Bradford, 2013; Sherman, Page-Dumroese, & Coleman, 2018) because, with thinning, much of the overstory structure is retained and less biomass is removed.

Insight about management impacts on soil biological processes is gained by measuring soil respiration ($R_s$) and soil exoenzyme activities. Soil respiration is an important indicator of soil metabolic activity including root and microbial respiration (Luo & Zhou, 2006), and as such is used as a soil quality indicator (Martínez-Salgado, Gutiérrez-Romero, Jannsens, & Ortega-Blu, 2010). Exoenzymes are secreted by microorganisms to breakdown common substrates to provide nutrients and energy. Assays of exoenzyme activities are indicators of microbial decomposition and nutrient cycling processes that are responsive to the soil chemical and physical environment (Burns et al., 2013). Thinning and slash removal have variable effects on $R_s$ (Jandl et al., 2007; Peng, Thomas, & Tian, 2008; Slesak, Schoenholtz, & Harrington, 2010). Thinning can reduce $R_s$, due to decreased root respiration (Mattson & Swank, 1989) or increase $R_s$ due to increased soil temperatures and C pools from decomposing roots and slash residue (Das Gupta & DeLuca, 2012). Studies on slash retention also have inconsistent $R_s$ results due to increased soil moisture, shading, and soil compaction (Cheng et al., 2014; Hendrickson, Chatarpaul, & Burgess, 1989; Kurth, Bradford, Slesak, & D’Amato, 2014; Mattson & Swank, 1989; Slesak et al., 2010).

Soil respiration can be influenced by N additions. In some ecosystems, N additions increase $R_s$ due to stimulation of fine-root respiration (Hopkins et al., 2013), but a meta-analysis found that forest soils tend to have decreased $R_s$ after N additions (Zhou et al., 2014). This reduction in $R_s$ following N additions has also been shown in N-limited forests, with the majority of the reduction occurring in the rhizosphere (Sun et al., 2014). Thus, $R_s$ response to management impacts may result from altered soil microbial metabolism due to changes in the physical or chemical environment.

Biomass removal can alter the environment and the activity of soil microbes, which could alter soil exoenzyme activity. Exoenzyme activity is dependent upon microbial production in response to soil chemical and physical environmental factors (Bowles, Acosta-Martinez, Calderon, & Jackson, 2014; Burns et al., 2013; Sinsabaugh, Hill, & Shah, 2009). Soil microbes produce exoenzymes in stoichiometric proportions that are dependent upon the availability of substrates and regulated by growth-limiting factors such as N availability (Sinsabaugh & Shah, 2012). For instance, microbes mediate N mineralization by regulating activities of cellulase ($\beta$-glucosidase), protease (aminopeptidase), and chitinase ($\beta$-N-acetyl-glucosaminidase; Ekenler & Tabatabai, 2004; Tabatabai, Ekenler, & Senwo, 2010). Activities of such C- and N-releasing exoenzymes are often correlated with activities of P-releasing exoenzymes (Bowles et al., 2014; Fatemi, Fernandez, Simon, & Dail, 2016; Shan, Coleman, & Kimsey, 2014), which effectively maintains balanced nutritional supply (Sinsabaugh & Shah, 2012). The response of exoenzyme activity to forest harvesting is not well understood. For instance, phosphatase activity decreases with harvest intensity in some studies (Hassett & Zak, 2005; Waldrop, McColl, & Powers, 2003), while others find that protease and phosphatase activities increase with retention of logging residue (Adamczyk et al., 2015). Exoenzymes respond to harvest disturbance when soil chemical factors also respond (Jones et al., 2010; Walker, Ward, & Jones, 2016), indicating the importance of soil chemical environment to microbial function.

Nitrogen is the main limiting nutrient in western North American forest soils (Coleman, Shaw, Kimsey, & Moore, 2014; Edmonds et al., 1989) and biomass removal can decrease N capital (Marshall, 2000), potentially modifying the activity of both C- and N-releasing exoenzymes. If biomass removal degrades site N capital, fertilizing forests may compensate for the loss (Helmisaari et al., 2011). In turn, N fertilization typically increases C- and P-releasing hydrolase exoenzyme activity with variable effects on N-releasing exoenzyme activity (Jian et al., 2016). Biochar may also mitigate the effects of biomass removal on soil microbial properties. Biochar is the charcoal produced through pyrolysis that is intentionally land...
applied to sequester C and enhance soil properties (Laird et al., 2010; Woolf, Amonette, Street-Perrott, Lehmann, & Joseph, 2010). The aromatic hydrocarbon in biochar is resistant to decomposition when added as a soil amendment (Spokas, 2010; Wang, Xiong, & Kuzyakov, 2016) so that it directly enters the stabilized soil C pools (Fang, Singh, Singh, & Krull, 2014; Wang, Chen, Wang, Zhang, & Zhang, 2018) and will therefore sequester C in the soil with long-term effects on soil properties. At forest sites, biochar can increase ground cover after disturbance, increase soil moisture, and decrease soil compaction associated with harvesting (Page-Dumroese, Coleman, & Thomas, 2017). For laboratory incubation studies, biochar decreases (Spokas, Koskinen, Baker, & Reicosky, 2009) or increases (Stewart, Zheng, Botte, & Cotrufo, 2013; Zheng, Stewart, & Cotrufo, 2012) CO2 emissions. However, comparisons of laboratory incubation studies and field studies show that CO2 emission responses to biochar are consistently higher in incubation studies than in field or greenhouse studies (He et al., 2017; Shen, Zhu, Cheng, Yue, & Li, 2017). The response of exoenzymes to biochar amendments have largely been conducted in laboratory incubations with variable results (Awad, Blagodatskaya, Ok, & Kuzyakov, 2012; Bailey, Fansler, Smith, & Bolton, 2011; Demisie, Liu, & Zhang, 2014; Ouyang, Tang, Yu, & Zhang, 2014). Smith (2013) conducted in-forest incubations of soil blended with biochar and found that biochar increases alanine aminopeptidase, decreased acid phosphatase, and β-N-acetyl-glucosaminidase and has no effect on β-glucosidase. The impact of biochar on enzymes may depend on the type of biochar, binding of substrate or products through surface interactions, microbial community structure, or environmental changes such as altered soil moisture or pH (Ameloot et al., 2014; Warnock, Lehmann, Kuyper, & Rillig, 2007).

In order to further understand the feasibility of small-diameter biomass removal for biofuel harvesting, we need regional, site-specific studies (Smith et al., 2000). Previously, we found the removal of biomass from forests in the intermountain region of northwestern United States known as the Inland Northwest did not diminish tree growth in the short term (Sherman et al., 2018). Here we address the impacts of biomass removal on forest R, and exoenzyme activity. If biomass removal from thinning operations impacts soil microbial processes, there could be implications for long-term tree growth. Our study had two objectives; first, to determine the impacts of thinning and biomass removal on R and exoenzyme activity, and second, to evaluate the ability of fertilizer and biochar soil amendments to compensate for potential effects from biomass removal on R and exoenzyme activity. We hypothesized that: (1) Relative to no-thin controls, post-thinning biomass removal would increase R and exoenzyme activity due to increased soil temperature and moisture availability; (2) Biomass retention would decrease R and exoenzyme activity due to decreased soil temperature caused by soil shading and insulation; (3) Soil amendments with biochar would increase soil respiration and exoenzyme activity relative to unamended control plots due to increased soil water, pH and organic matter; and (4) N fertilization would decrease N-releasing exoenzyme activity due to higher soil N availability.

2 | MATERIALS AND METHODS

2.1 | Site characteristics

This study included two Inland Northwest locations: one at Pitwood and the other at University of Idaho Experimental Forest (UIEF; Figure 1). Both locations were regenerated mixed-conifer forests with volcanic ash containing silt-loam soils. The Pitwood location (46.983104, −116.483943) was a 22-year-old mixed conifer forest of mostly Douglas-fir (Pseudotsuga menziesii (Mirb.) Franco var. glauca (Beissn.) Franco), grand fir (Abies grandis (Douglas ex D. Don) Lindl.), and western redcedar (Thuja plicata Donn ex D. Don) growing at 1,000 m elevation in an Andisol soil classified as ashy over loamy, amorphic over isotic, frigid Typic Udihumite (Flewite soil series; Soil Survey Staff 2011). The well-drained deep soil was formed from fine-grained quartzite parent material with a thick mantle of volcanic ash. Pitwood was managed by PotlatchDeltic Corporation as a commercial forest with a rotation period of approximately 40 years. UIEF (46.849512, −116.845068) was a 25-year-old naturally regenerated mixed conifer stand of ponderosa pine (Pinus ponderosa Douglas ex P. Lawson & C. Lawson), Douglas-fir, grand fir, lodgepole pine (Pinus contorta Douglas ex Loudon), and western larch (Larix occidentalis Nutt.) growing at ~860 m elevation in an Alfisol classified as coarse-silty, mixed, superactive, frigid Vitrandic Fragiorthol (Santa series; Soil Survey Staff 2011). The deep loess soil contains volcanic ash on the surface and overlays granite bedrock. The UIEF study location was managed by the University of Idaho as a commercial forest with a harvest rotation period of 45−50 years. A detailed description of the experimental design is reported by Sherman et al. (2018). Below we provide a brief description of the experimental treatments.

2.2 | Biomass treatments

At each location, we had two replicate stands. Each replicate stand was divided into four biomass treatments, including three thinned whole-plots with different biomass retention levels and one unthinned control whole-plot. Each whole-plot
contained four split plots (see Section 2.3). In spring 2013 the biomass retention plots were thinned from below to approximately 5-m spacing, leaving ~400 trees per hectare. The thinned area was divided into three whole-plots each with different biomass retention levels: full biomass removal (0×), full biomass retention (1×), and double biomass retention (2×). In the 2× treatment, residue from 0× plots was added to the residue that had been retained from thinning.

2.3 | Soil amendments

Four soil amendment treatments were randomly assigned within each whole-plot to one of four 40 × 40 m split-plots with a total of 64 study plots (2 locations × 2 replicate stands × 4 biomass treatments × 4 amendments). A 20 × 20 m measurement plot with a 10 m treatment buffer was established within each treatment plot. The amendment treatments were urea fertilizer (F), biochar (B), fertilizer plus biochar (FB), and an unamended control (C). Nitrogen fertilizer was applied as urea at 224 kg N/ha to the F and FB plots. Fertilization occurred in May 2014 at Pitwood and in November 2013 at UIEF. Biochar was obtained from Evergreen Forest Products (Tamarack, ID) and was produced from mixed conifer mill residue at 980°C. Biochar was surface applied at 2.5 Mg/ha to each B and FB plots of the first replicate stand at UIEF in October 2013, to the second replicate stand at UIEF in April 2014, and to both replicate stands at Pitwood in May 2014.

2.4 | Exoenzyme activity

Laboratory assays determined soil exoenzyme activities. Soil samples were collected each spring (April), summer (July), and fall (October) of 2015 and 2016. Samples (5 cm diameter) were taken to 15 cm depth from a randomly selected location within each measurement plot. Field-collected samples were held on ice during transport to the laboratory where they were refrigerated before processing within 48 hr. Samples were sieved through a 2 mm screen to remove roots, twigs, and stones, and to homogenize.

Exoenzyme activities were measured with fluorescent microplate assays (Saiya-Cork, Sinsabaugh, & Zak, 2002; Shan et al., 2014). For each sample, the activities of alanine aminopeptidase (AM), β-glucosidase (BG), β-N-acetyl-glucosaminidase (CH), and acid phosphatase (PH) were determined and expressed in nmol g⁻¹ hr⁻¹ using DeForest's (2009) calculations. All exoenzyme assays were conducted in acetate buffer adjusted to pH 5.5 and incubated at 20°C. Length of incubation varied by enzyme: 2 hr for CH, 3 hr for BG, 4 hr for PH, and 6 hr for AM.

2.5 | Soil organic matter and pH

Soil organic matter content and pH were measured commercially (AgSource Cooperative Services, Harris Labs) for each exoenzyme sample collected during the study. Soil organic matter content was measured using loss on ignition.
Soil pH was measured (1:1, v:v, soil to water) with ion electrodes.

2.6 | Soil respiration

\( R_s \) was measured each spring, summer, and fall of 2015 and 2016 in three randomly selected locations within each measurement plot. \( R_s \) was measured using a LI-COR LI-6400 with a 6400-09 soil chamber (LICOR) and an EGM-5 with a SRC-2 Soil Respiration Chamber (PP-Systems). The LI-COR device was used in 2015, and to increase measurement efficiency, both the LI-COR and PP-Systems devices were used in 2016 with each instrument measuring one or two sample locations per plot. Accuracy between the devices were tested in the field and found to yield similar results, which agreed with previous studies (Pumpanen et al., 2004). The three \( R_s \) measurements were averaged for analysis.

2.7 | Soil moisture and temperature

Soil moisture content was measured in the laboratory for each soil sample using a moisture balance (HB43-S Mettler-Toledo). Field soil moisture and temperature were measured along with each \( R_s \) measurement at 15 cm soil depth using a soil moisture probe (HydroSense II, Campbell Scientific) and a soil temperature probe (6000-09TC Soil Probe Thermocouple, Li-Cor).

2.8 | Statistical analysis

A repeated measures analysis of covariance (ANCOVA) was performed for each variable using R (‘lme’ function in ‘nlme’ package Pinheiro, 2018). Each model included four experimental factors as well as interactions among them: location (\( n = 2 \)), season (\( n = 3 \)), biomass treatment (\( n = 4 \)), and soil amendment (\( n = 4 \)). Two replicate stands were included within each location. Plot was used as the random factor. Season by year was the repeated measure factor. Four dependent variables were evaluated after being natural-log transformed to meet equal variance and normality assumptions. The N-release-dependent variable included the log-transformed sum of AM and CH activities. P-release used log-transformed acid phosphatase activity (PH). Log-transformed BG activity was used as a covariate for \( R_s \), N-release, and P-release to represent the dependence of \( R_s \) and enzymatic nutrient release on cellulose decomposition (Mariscal-Sancho, Santana, Mendiola, Peregrina, & Espejo, 2010; Moorhead, Rinkes, Sinsabaugh, & Wintraub, 2013; Sinsabaugh et al., 2009).

Stepwise regression was used to determine additional covariates (soil moisture, soil temperature, soil pH, soil organic matter) to include in each model using the stepAIC function in the ‘MASS’ package (Venables & Ripley, 2002). Model variations with lowest AIC were selected to perform each ANCOVA analysis.

Fully parameterized models—including all interactions (up to seven-way) among covariates and experimental factors—were difficult to interpret, and only improved model fit (AIC) by 0.5%. Therefore, we simplified models to include experimental factor main effect, interactions among experimental factors, and covariates. If higher order interactions among experimental factors were not significant, they were eliminated. Post hoc tests to determine differences between treatment factors and interactions were calculated using the pairwise function derived in the ‘lsmeans’ package (Lenth, 2016). Correlation coefficients for continuous variables were calculated using the ‘lm’ function in the ‘stats’ package to evaluate variability (R Development Core Team, 2018).

3 | RESULTS

We found consistent responses of \( R_s \) and exoenzyme properties to independent experimental and environmental covariates. Independent factors explaining variation in respiration and exoenzyme properties included location, season, BG activity, soil moisture, soil temperature, and pH (Table 1). However, most response variables were insensitive to biomass or amendment treatments, except \( R_s \), where the response to amendment treatments varied between locations (A × L \( p = .02 \)). Most variables examined were positively correlated with each other, except temperature, which was negatively correlated with soil moisture and soil organic matter (Figure 2). Both CH and AM exoenzymes release N, and we used their sum to represent N-release. While CH accounts for most of the correlations with other variables, the addition of AM was found to slightly increase correlations with soil moisture content and soil organic matter.

3.1 | Soil environment

Sherman et al. (2018) report results of soil temperature and moisture collected at the field locations. In general, spring soil temperature is mild with high moisture, summer is hot and dry, and fall is cool with increasing moisture. Soil temperatures during the experiment averaged 3°C higher at UIEF than Pitwood and 5°C higher during summer than spring and fall. Seasonal physical environment varied by location; UIEF was warmer in the spring and summer and cooler in the fall compared to Pitwood. Physical soil environmental variables did not respond to biomass or amendment treatments.

Soil chemical environment, as measured with pH and organic matter, was marginally affected by soil amendment. Fertilization
tended to decrease pH while biochar tended to increase it (Figure S1c). Amendment treatments were mainly dependent upon location and season (Table S1). Soil pH was 6.24 ± 0.04 at Pitwood and 5.82 ± 0.04 at UIEF (Figure S1a) and it varied 0.2 units between summer and fall (Figure S1b). Seasonal differences depended on location. At Pitwood, pH in spring and summer were equivalent and both were higher than fall. While at UIEF, pH tended to be higher in summer (Figure S1d).

Response of soil organic matter to biomass and amendment treatments depended on location, and season (Table S1). Organic matter was typically 0.5% higher at Pitwood than UIEF and surprisingly it was significantly higher (>0.12%) during summer than spring or fall. Variation due to season and experimental treatments appeared to result from high values in some B and FB plots at Pitwood during summer and relatively low C values at Pitwood during spring and at UIEF during fall (Figure S2).

3.2 | β-Glucosidase activity

BG activity did not respond to biomass nor amendment treatments. The seasonal response of BG activity was dependent upon locations (Figure 3). At Pitwood, summer BG was higher than spring and fall. While at UIEF, spring BG activity was lower than fall and summer (L × S p = .09 Table 1). BG activity was affected by soil moisture content, soil organic matter content, and soil temperature (Table 1). Moisture content and temperature explained most variation in BG activity (F > 38).
Nitrogen release

N-release had a seasonal effect at UIEF, with summer having higher N-release activity than spring and fall (Figure 4), while, no seasonal response of N-release was apparent at Pitwood (L × S p < .01). N-release was correlated with BG activity, soil moisture content, soil organic matter, and soil temperature (Table 1). BG activity was the highest covariate predictor of N-release (F = 130.52; R² = .43, Figure S3) indicating interdependence among exoenzyme activities.

Phosphorous-release

The response of P-release to treatments and season was consistent between locations. Neither biomass nor amendment treatment responses were observed. Pitwood had marginally higher P-release activity than UIEF (Table 1). The highest P-release was in summer (p < .01, Figure 5), with no differences between fall and spring. Phosphorous release was
positively correlated with BG activity (Figure 6), soil moisture content, and soil temperature (Table 1, Figure 2).

The response of $R_s$ to amendments varied by location (Table 1, Figure 7). At Pitwood, the amended plots had lower $R_s$ than the unamended control plots. While at UIEF, the amended plots had higher $R_s$ than the control plots ($A \times L p = .02$). However, post hoc mean comparison tests found no difference between amendments within the locations. There were also seasonal differences in $R_s$ that varied between locations (Figure 8). At Pitwood, $R_s$ peaked in the summer, and at UIEF, $R_s$ was highest in the spring and lowest in the fall ($L \times S p < .0001$). Soil organic matter was the most significant covariate affecting $R_s$ ($F = 44.4$; Figure 9), but all covariates in the model were significant and positively correlated with $R_s$ (Table 1, Figure 2).

4 | DISCUSSION

Our results indicate that $R_s$ and exoenzyme activities in the Inland Northwestern forests may be resilient to small-diameter biomass harvesting and compensating amendments. $R_s$ and exoenzyme activities were not significantly altered by biomass retention levels or soil amendments (Table 1). This lack of response suggests that forest management for bioenergy production in this region is feasible without negative consequences to belowground processes. Though there were no management effects, there were many significant responses to location and season, and correlations between response variables and environmental factors. The significant responses demonstrate the precision of the experimental design, the correlations confirm understanding of exoenzyme activity, and together they provide insight to the long-term effects of biomass removal and use of compensating soil amendments.

4.1 | Biomass removal and slash retention

We hypothesized that $R_s$ would increase in response to thinning and biomass removal due to increased soil temperature, and that $R_s$ would decrease from biomass retention due to shading and insulation of the soil. We did not see any
differences of $R_s$ rates among biomass treatments. Lack of $R_s$ response is likely due to the lack of temperature and moisture response to biomass treatments because of the strong influence these soil physical environmental variables have on $R_s$ (Luo & Zhou, 2006; Peng et al., 2008). There were physical environmental responses to location and season with corresponding responses of $R_s$, yet, biomass treatments within location did not affect soil moisture or temperature (Sherman et al., 2018). Others suggest that increased heterotrophic respiration from increased temperature (Mattson & Swank, 1989) or increased decomposition of belowground detritus (Vesala et al., 2005) is balanced by lower autotrophic (root plus mycorrhizal) respiration (Mattson & Swank, 1989). Such trade-offs with temperature are unlikely in our study because we did not see increased temperatures (Das Gupta & DeLuca, 2012). It would be necessary to distinguish heterotrophic and autotrophic respiration to test if they responded uniquely to biomass treatments.

Slash retention plots may have experienced increased soil moisture and temperature due to thinning. Yet, slash also provides shade, which decreases radiation load and moderates midday temperature increases found with slash removal and thereby deceases $R_s$ (Moroni, Carter, & Ryan, 2009; Slesak et al., 2010). We did not observe such changes in the physical environment due to slash retention and conclude that the lack of $R_s$ response to slash is due to lack of environmental response to biomass treatments.

Results also do not support our hypothesis that biomass removal affects exoenzyme activity. Our lack of exoenzyme response to biomass treatments may be due to the absence of soil chemical response. Soil pH and organic matter were equally unresponsive to biomass treatments. Soil pH and organic matter are known as factors that regulate exoenzyme activities over broad scales (Sinsabaugh et al., 2008). When clear-cut harvests do not influence soil chemistry, exoenzyme activities also do not respond (Jones et al., 2010). Yet, when soil chemistry responds to harvest, exoenzyme activities also respond (Geng, Dighton, & Gray, 2012; Walker et al., 2016). If biomass treatments substantially affect soil chemical environment we should expect a response of exoenzymes.

4.2 Soil amendments

We reject our hypotheses that $R_s$ and exoenzyme activity react in opposite directions for amendments of biochar versus N fertilizer. Instead, the direction of $R_s$ response was consistent for biochar and N fertilizer at both locations, and it was different locations that resulted in opposite $R_s$ responses to soil amendments. The different directional response of $R_s$ to N fertilizer and biochar are not unique. $R_s$ is known to respond to N fertilization by decreasing (Janssens et al., 2010; Lee & Jose, 2003; Olsson, Linder, Giesler, & Hogberg, 2005; Sun et al., 2014), increasing, at least in the short term (Jia, Wang, Li, Zhang, & McLaughlin, 2011; Peng et al., 2011; Ryan, Hubbard, Pongracic, Raison, & McMurtrie, 1996; Wang, Peng, & Fang, 2010), or to have no effect (Micks, Aber, Boone, & Davidson, 2004). The responses of $R_s$ to biochar amendments are equally complex (He et al., 2017; Li et al., 2018; Sarauer, Page-Dumroese, & Coleman, 2019; Smith, Collins, & Bailey, 2010). Our results showed that the response of $R_s$ to amendments was site specific, although the site factors controlling the variable responses are uncertain. $R_s$ impacts from N or biochar additions are often attributed to changes in microbial biomass and activity (Geisseler, Lazicki, & Scow, 2016; Lehmann et al., 2011). Yet in our study this is not a likely explanation because we did not see a similar response of microbial activity to amendments based on effects of the main exoenzymes that release C, N, and P. While there were enzymes we did not measure, those that were included are most active and represent the main decomposition pathways (Dick & Kandele, 2005). No environmental or exoenzyme variables correlated with opposing $R_s$ response to amendments between locations. Location differences in OM were better correlated with lower $R_s$ than with exoenzyme activities. These contrasting results showing an $R_s$ response to fertilization that varies by location but with no corresponding exoenzyme or environmental response, suggest that greater understanding of underlying processes is necessary before biochar or fertilization was routinely used to compensate for effects of biomass removal.

The response of exoenzyme activity to biochar also depends on soil series, biochar type, amendment rate, season, and exoenzyme assayed (Awad et al., 2012; Bailey et al., 2011; Demisie et al., 2014; Ouyang et al., 2014; Page-Dumroese et al., 2017; Smith, 2013). Biochar is highly porous and has been shown to alter soil water-holding capacity, increasing seasonal soil moisture (Lehmann et al., 2011; Page-Dumroese et al., 2017), which can impact $R_s$ rates. However, our study locations have ash-laden soils. The porosity of soils containing volcanic ash also increases water-holding capacity due to high porosity and fine texture (Meurisse, Robbie, Niehoff, & Ford, 1991), which in turn may impact $R_s$ and exoenzyme activity. Since biochar adds porosity like that of ash, it may explain why we did not find differences in our biochar amended plots compared to control plots. We previously found no soil moisture, soil temperature, or forest growth effect in response to biochar applications at our locations (Sherman et al., 2018), so we were not surprised that there was no response of $R_s$ and exoenzyme activity to biochar. The lack of biochar effect on $R_s$ and exoenzyme activity may also be due to the relatively small quantity of biochar applied to our plots (2.5 Mg/ha), which was equal to the amount that could be produced from 10 Mg/ha of biomass. Comparative analyses indicate typically greater effects on $R_s$ and exoenzyme activity with increasing amendment rates (He et al., 2017; Page-Dumroese et al., 2017).
Our study found BG activity to be positively correlated with $R_s$. BG activity is often used as a soil quality indicator due to its role in releasing glucose as a labile energy source to maintain soil microbial metabolism and its relation with soil organic matter, and disturbance (Dick & Kandele, 2005; Martinez-Salgado et al., 2010). It follows that an exoenzyme that cycles C would correlate with CO$_2$ emissions. Mariscal-Sancho et al. (2010) found a strong correlation between BG activity and $R_s$ in a disturbance-gradient study with Ultisols. Moorhead et al. (2013) found that the sum of C degrading exoenzymes correlated with microbial respiration in laboratory incubations with two distinct Entisols. Our study is the first of our knowledge to show the BG-$R_s$ correlation in coniferous forests. We found BG activity was also highly correlated with AM + CH and phosphatase activity in this study, supporting findings that exoenzymes involved in both N and P cycling are colimiting factors in decomposition rates (Schimel & Weintraub, 2003; Sinsabaugh et al., 1993).

### 4.4 Soil pH

Soil pH did not influence response of exoenzyme activities or correlate with any of the individual exoenzymes measured. Sinsabaugh et al. (2009) showed clear correlations between soil exoenzymes activity, and soil pH, soil organic matter, and climatic factors. Our results agreed by showing correlations between exoenzyme activities and climatic measures, such as soil moisture and temperature. We also show significant correlations with organic matter content for BG and the N-cycling exoenzymes. We believe our lack of pH correlation was due to the small range of soil pH that was measured in our plots (Figure S1), and we assume that if we measured exoenzymes in soils with a broader pH range, we would have seen a pH effect.

We did find a positive correlation between $R_s$ and pH. Previous studies show increasing $R_s$ with pH (Andersson & Nilsson, 2001; Sitaula, Bakken, & Abrahamsen, 1995). This result is likely related to soil alkalinity’s potential to impact soil microbial biomass (Acielo Pietri & Brookes, 2009; Sawada, Funakawa, & Kosaki, 2009) and plant growth, which directly affects root respiration (Hall, Paterson, & Killham, 1998). Both soil pH and $R_s$ were higher at Pitwood compared with UIEF which likely contributed to the positive correlation observed between these variables. In contrast, the marginally significant response of pH to amendments showed only 0.17 pH change among treatment averages compared to the highly significant response of pH to location that showed a 0.41 pH difference between Pitwood and UIEF. Soil pH appears to be an important indicator of management impacts on forest $R_s$ and exoenzyme activity.

### 5 CONCLUSIONS

Our study indicates that thinning, biomass removal for biofuel production, or amendments will not impact $R_s$ and exoenzyme activities in the first 3 years after harvesting. Paired with our previous findings that biomass removal did not impact tree growth (Sherman et al., 2018), the initial findings of this project suggest that removing biomass for bioenergy from overstocked forests in the Inland Northwest would not harm forest growth, $R_s$, or exoenzyme activity. A follow-up study to measure long-term tree growth, $R_s$ and exoenzyme activity is critical to understanding if observed short-term responses are sustained.

Our results also show that $R_s$ and exoenzyme activity are sensitive to soil physical and chemical environmental factors. $R_s$ and exoenzyme activity vary by location and season, as does the physiochemical environment, which demonstrates impacts of management practices are smaller than the relatively subtle effects of location and season. Soil physical and chemical environmental factors were largely unaffected by management treatments. If management causes significant soil environmental impacts in the future, or in other management operations, it is likely that tree growth, $R_s$, and exoenzyme activities will also be affected.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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