

Fall prescribed burns deplete surface soil C pools more than spring burns in a young mixed-conifer forest

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ABSTRACT

Wildfires burn as much as ~6 % of Earth's ice-free land annually and remove carbon (C) stored in surface soils. Prescribed burns may offer an opportunity to preserve soil C stocks by limiting the extent and severity of wildfires. However, prescribed burns in western North America are mostly conducted during short windows in the early fall season. Expanding burning to other seasons, like spring, is key to increasing effectiveness. Yet, it is not clear how burning stands in the spring versus the fall affects soil C stocks, a key consideration for managers seeking to preserve soil C. To assess how burn season affects soil C dynamics, we measured bulk soil C, mineral associated organic C (MAOC), particulate organic C (POC), pyrogenic organic matter (PyOM), microbial respiration, and extracellular enzyme activity in surface soils for two years after burning young mixed-conifer forest stands in either the fall or spring. We found that fall burning, which consumed more surface fuels, immediately combusted soil organic matter, lowering POC from 37 ± 14 to 14 ± 8.3 g C kg⁻¹ three days after burning. Furthermore, fall burning stimulated microbial respiration, preventing bulk C from increasing above 43 ± 14 g C kg⁻¹ for two years. Spring burning did not immediately decrease soil C, and increased C by 64 % two years after the fire, potentially due to suppressed microbial respiration allowing C to accumulate. Taken together, our results suggest that spring prescribed burns preserved soil C stocks relative to fall burns in young mixed-conifer forest stands.

1. Introduction

Wildfires burn as much as ~6 % of Earth's ice-free land annually and are becoming more severe with global change, wildfire suppression, and fire-use exclusion (Abatzoglou et al., 2019; Chen et al., 2023; Ellis et al., 2022; Jones et al., 2020; Riley and Loehman, 2016). Severe fires can deplete carbon (C) in surface soils, which store more C than plants and the atmosphere combined (Sanderman et al., 2017). A critical solution to decrease the extent and severity of wildfires and preserve soil C is to conduct low-severity prescribed burns and reduce the amount of primary surface fuels that often lead to severe fires (Jones et al., 2025; Ryan

et al., 2013). Conventionally, the early fall season is a desired window for burning because it is aligned with the historic fire season, and fuels are often at an ideal soil moisture to allow burning while limiting the unintentional spread of fire (Ryan et al., 2013). Constraints around permitting, however, severely limit burning in the fall (York et al., 2020). To meet the increasing demands for fuel reduction treatments, it will be necessary to conduct more prescribed burns, including in the spring, a period outside of the historical summer and fall fire regime in much of the United States (Ryan et al., 2013). Yet, burning outside of the historical fire season may have unintended consequences for important ecosystem services like soil C sequestration. Soil C can be depleted when

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fires combust organic matter (Walker et al., 2019; Wardle et al., 2003), or when microbial respiration outpaces plant C inputs following burning (Krichels et al., 2025; Pellegrini et al., 2021b). Understanding whether the season in which prescribed burns are conducted affects soil C dynamics is necessary to understand how managers can preserve key ecosystem services while meeting demands to reduce forest fuel accumulations at larger spatial scales and higher frequencies.

Fire can combust soil organic matter (SOM) and release soil C to the atmosphere as carbon dioxide (Walker et al., 2019; Wardle et al., 2003). While SOM combustion is a major pathway of soil C loss during wildfires, prescribed burns may not transfer enough heat belowground to combust much SOM (Alcañiz et al., 2018; Fontúrbel et al., 2021), minimizing soil C losses. However, soil particulate organic C (POC) combusts at lower temperatures than mineral-associated organic C (MAOC), allowing prescribed burns to preferentially combust POC despite lower burn intensity (Wang et al., 2023). If prescribed burns preferentially deplete POC, then MAOC may account for the majority of soil C in burned landscapes, where it is more likely to persist because mineral associations also protect C from microbial decomposition (Lavallee et al., 2020; Krichels et al., 2025). Burning can also stimulate the production of pyrogenic organic matter (PyOM), which is relatively resistant to microbial decomposition and can persist in soils for centuries (DeLuca et al., 2020; Leuthold et al., 2025; Licata and Sanford, 2012; Pingree et al., 2012). However, PyOM formed during low-severity prescribed burns may not protect soil C to the same extent as PyOM formed during high-severity burns (Li et al., 2025). Thus, predicting how prescribed burns affect soil C stocks requires understanding how heat and microbial respiration affect POC, MAOC, and PyOM pools in burned soils.

Whether the C that is not combusted during prescribed burns persists in soils depends on subsequent respiration dynamics by microorganisms (Krichels et al., 2025; Pellegrini et al., 2021a). Microbial mortality following burning can decrease microbial biomass (Pulido-Chavez et al., 2022; Whitman et al., 2019) and slow respiration in the years after burning. However, some fire-resistant, pyrophilous (or “fire-loving”) microorganisms can massively increase in abundance after fire, either because they survive the burn or because they reproduce fast and are able to colonize in the absence of competitors, potentially allowing for microbial respiration to persist despite fire-induced mortality (Enright et al., 2022; Pellegrini et al., 2021a; Pulido-Chavez et al., 2022; Wang et al., 2012; Whitman et al., 2019). Moreover, burning can break down chemically complex SOM and microbial residues into more bioavailable C compounds (VanderRoest et al., 2024), potentially enhancing respiration by pyrophilous microbes and stimulating soil C losses (Catalanotti et al., 2018). Alternatively, fire may increase the proportion of MAOC and PyOM-C that is resistant to microbial respiration in burned soils, slowing C losses. Given the potential for prescribed burning to either accelerate or slow microbial respiration, understanding controls over microbial activity following fire is important to predict the fate of soil C after prescribed burns.

Prescribed burns are often conducted in the late summer or fall to align with the historical fire regimes of western US forests (Ryan et al., 2013; Stephens and Collins, 2004). To meet the increasing demand to reduce forest fuel loads, however, prescribed burns have been conducted in spring, when live fuels and soils are expected to have higher moisture content than in fall (Ryan et al., 2013). Soil moisture content at the time of burning may determine how soil C responds to fire. For example, Microbial mortality may increase if burning moist spring soils transfers heat belowground more efficiently than burning dry fall soils (DeBano, 2000), decreasing microbial respiration and allowing C to accumulate. Alternatively, higher moisture content in spring may hinder the combustion of above ground biomass and, thus, suppress belowground heat transfer compared to dry fall conditions (Badía et al., 2017), slowing the combustion of POC while allowing microbial respiration to persist. To assess how burn season affects soil C dynamics, we ask: i) does burning young forest stands in the spring instead of the fall decrease how much

POC is combusted? And ii) how does burning young forest stands in the spring versus the fall affect microbial activity and the persistence of soil POC and MAOC in the months after burning?

We answered these questions by incubating soils in the lab and monitoring microbial respiration, extracellular enzyme activity (an index of decomposition potential), ash depth (an index of soil burn severity), bulk soil C, PyOM-C, MAOC, and POC for six timepoints ranging from pre-fire, to two weeks, and to two years after burning young mixed-conifer forest stands in either the spring or fall. We hypothesized that wetter conditions and lower temperatures associated with spring burning would decrease soil burn severity compared to fall burning, limiting C losses from combustion without affecting microbial respiration. We also hypothesized that drier and warmer fall soils would increase soil burn severity, combusting more POC than spring burns, forming more PyOM, and providing microorganisms with a flush of labile C to stimulate decomposition and C losses in the months after burning. Finally, we hypothesized that MAOC would be resistant to prescribed burns and microbial decomposition, allowing it to persist regardless of burn season.

2. Methods

2.1. Site description

This study took place in the Blodgett Forest Research Station (BFRS; managed by the Center for Forestry at UC Berkeley), a mixed-conifer forest in the North-Central Sierra Nevada mountains (38° 54' 45" N, 120° 39' 27" W). Eight stands (0.4-ha–0.8-ha) were randomly chosen to either be burned either in the fall (November 13, 2019, $N = 4$) or the spring (April 28–May 1, 2020; $N = 4$) (York et al., 2022); stands were between 1275 and 1325 m above sea level. Fall burning is defined as occurring after the summer drought, but prior to the saturation of fuels from multiple winter storms. Generally, this occurs at BFRS in October or November, following one or two storms but prior to accumulating 13 cm of total precipitation. Spring burning is defined as occurring following heavy winter storms but prior to the drying out of fuels in the early summer to a point that precludes burning within a predetermined fuel moisture prescription. We used the same weather and fuel moisture prescription for both fall and spring burns: 10-hour fuel moisture was 8–10 %; relative humidity was 36–40 %; temperature was 13–17°C. Pre-fire treatment history was the same across all stands, as was stand age.

One additional stand was monitored as a control. While only having one control stand may limit statistical inference, the large plot size and sampling of multiple subplots means that the control stand should be representative of baseline conditions. Furthermore, by sampling each stand multiple times before and after burning, we can assess how soil C pools and microbial activity change over time in response to fire in addition to comparing burned to control stands. In the control stand, gravimetric soil moisture averaged $0.18 \pm 0.021 \text{ g H}_2\text{O g}^{-1}$ within three days of the fall burn and $0.46 \pm 0.058 \text{ g H}_2\text{O g}^{-1}$ within three days of the spring burn (Figure S1). All stands consisted of 12–13-year-old conifer species, including sugar pine (*Pinus lambertiana*), ponderosa pine (*P. ponderosa*), white fir (*Abies concolor*), incense-cedar (*Calocedrus decurrens*), and Douglas-fir (*Pseudotsuga menziesii*). Soils at the site are mesic Ultic Haploxeralfs in the Holland series (Soil Survey Staff, 2019). The forest has a Mediterranean climate with cool winters (average temperature 0–9 °C) and warm dry summers (average temperature 14–32 °C). During the time of our study (2018–2020), wet season precipitation was 145 cm yr^{-1} , and the mean annual air temperature was 6.2 °C with a daily maximum and minimum of 10.9 °C and 2.6 °C (York et al., 2022). In this region, fire was common (less than every 12 years at the stand scale) prior to the early 20th century, when fire exclusion policies were implemented (Stephens and Collins, 2004).

2.2. Soil sampling

Soil samples were collected from all stands prior to burning (October 3, 2019) as well as 3 days, 24 days, 6 months, 1 year, and 2 years after burning the fall stands, and 1 day, 24 days, 1 year, 1.5 years, and 2 years after burning the spring stands. Soils were not collected one day after the fall burn because they were too hot to handle. Later, slightly different timepoints in the spring were sampled due to inclement weather and snowfall. Three days after each burn, we measured and averaged ash depth from three locations per 1-m² subplot as a proxy for soil burn severity as previously established (Glassman et al., 2023; Pulido-Chavez et al., 2022). While we did not measure soil temperature to corroborate burn severity, ash depth increases with soil heating (Parson et al., 2010) and fire severity (Bodí et al., 2014) and has been used as an index to relate soil burn severity to post-fire microbial communities (Pulido-Chavez et al., 2022). Soil samples (0–10 cm) were collected from the A-horizon after completely removing either the ash or the organic forest floor layer. Soil samples were collected with ethanol-cleaned releasable bulb planters from 1-m² subplots located 13, 17, or 20 m north or south from the center of each stand (six subplots per stand). The samples were immediately transported back to the University of California, Riverside (UCR). Water holding capacity (WHC) was determined by saturating soil samples with water and measuring how much water they retained against gravity over a 16-hour incubation in a closed environment to minimize losses to evaporation.

2.3. Soil C fractions

Density fractionation was used to measure the amount of C in particulate organic matter (POM) and mineral associated organic matter (MAOM) from soils collected from one of the north subplots (all subplots had similar aspect and slope) within each of the burned stands and from four of the subplots in the control stand at each timepoint (12 subplots by 6 timepoints = 72 samples) according to Püspök et al. (2022). We sieved (2-mm) soil prior to analysis and oven-dried 5 g of soil at 60 °C overnight before adding to 25 mL of a 1.65 g L⁻¹ sodium polytungstate solution (SPT). The soil in this solution was then dispersed using 200 J mL⁻¹ ultrasonic energy at 60 W. To separate POM from MAOM, the solution was centrifuged at 2500 ×g for one hour. The floating fraction was then aspirated onto a pre-ashed 0.45-µm glass fiber filter before being washed with 20 mL of ultrapure water to remove residual SPT; this soil was oven dried and weighed to measure POM mass. The remaining soil pellet was washed with ultrapure water before passing through a 53-µm sieve to separate MAOM (< 53 µm) from sand (> 53 µm). POM, MAOM, and sand fractions were then analyzed for soil C and N concentrations using an elemental analyzer (Flash EA 1112 CN; Thermo Fisher Scientific Inc.). The sand fraction had very low soil C (1.54 ± 0.97 g C kg⁻¹ dry soil; less than 4 % of bulk C) and is not presented in this manuscript. On average, we recovered 103 ± 5.3 % of soil mass and 92 ± 21 % of soil C.

We digested non-pyrogenic organic matter in soils samples with weak nitric acid and hydrogen peroxide and measured the remaining organic matter as an estimate of the concentration of PyOM (Kurth et al., 2006; Licata and Sanford, 2012; Pingree et al., 2012). Oven dried soil samples (1 g at 60 °C) were mixed with 10 mL of 1 M nitric acid and 20 mL of 30 % hydrogen peroxide in a 100 mL digestion tube. The solution digested at room temperature for 5 min, at 100 °C for 16 h, and then was cooled before filtering (Whatman #2). The remaining soil was then dried before being analyzed for C content, which was used to calculate PyOM-C.

2.4. Microbial respiration

Microbial respiration was measured from soil samples from one of the north, and two of the south subplots from each of the nine stands after wetting to 50 % water holding capacity. To do this, 10 g of sieved

soil was placed in a 237-mL glass jar, water was added to raise moisture to 50 % of WHC, and the jar was closed with a lid fitted with a rubber septum. A gas sample (~2 mL) was removed from each jar and analyzed for CO₂ concentrations using an infrared gas analyzer (LI-COR LI-810; LI-COR Environmental; Lincoln, NE) one hour after the jar was closed; a separate gas sample was taken from the ambient lab air when each jar was closed. This was repeated 1, 3, 6, 24, 30, 48, 54, 72, 78, and 96 h after wetting the soil in the jar. Microbial respiration was calculated as the difference between the initial (ambient) and final (one-hour) CO₂ concentrations for each of the timepoints. Cumulative CO₂ emissions for each sample over the 96-hour incubation were calculated using trapezoidal integration.

2.5. Potential extracellular enzyme activity

The potential activity of hydrolytic extracellular enzymes was measured from three subplots from each plot using substrates labeled with fluorescing methylumbelliferone (MUB) or 7-amido-4-methylcoumarin (MC) (Marx et al., 2001). Specifically, the potential activity of the starch-degrading enzyme α-glucosidase (AG), the cellulose degrading enzyme β-glucosidase (BG), the cellulose degrading enzyme 1,4-β-cellobiohydrolase (CBH), the chitin degrading and N acquisition enzyme N-acetyl-β-D-glucosaminidase (NAG), the peptide degrading and N acquisition enzyme L-Leucine aminopeptidase (LAP), and the organic P degrading and P acquisition enzyme Phosphomonoesterase (PHO) were measured using the following fluorescing substrates: 4-MUB-α-d-glucopyranoside for AG, 4-MUB β-d-glucopyranoside for BG, 4-MUB-β-D-cellobioside for CBH, 4-MUB N-acetyl-β-D-glucosaminide for NAG, L-Leucine-7-amido-4-methylcoumarin for LAP, and 4-MUB--phosphate for PHO.

Potential enzyme activity was measured using assays conducted in 96-well plates with 100 µL substrate and 100 µL soil slurry. Soil slurries consisted of soils (1:125 soil weight to volume) in a universal buffer solution at pH 6.5. The background fluorescence of soils and substrate were measured for each substrate as was the quenching of MUB by soils. Fluorescence was measured at 360 nm excitation and 460 nm emission in a plate reader (Tecan, Männedorf, Switzerland) five times over a 3-h period (McLaren et al., 2017; Saiya-Cork et al., 2002).

Activity of the oxidative enzymes phenol oxidase (Phenol) and peroxidase (Perox) was measured using L-3,4-dihydroxyphenylalanine substrate. After a 24-h incubation, color absorbance was measured at 460 nm.

2.6. Statistical analyses

All statistics were conducted using R (R Core Team, 2023). We used linear mixed effects models (lme4 package; Bates et al., 2015) to assess if MAOC, POC, total C, EEA, or microbial respiration changed over time in burned and control plots; stand and sampling location were included as random effects to account for study design. We treated time since burning as a categorical variable so that we could assess how each timepoint compared to pre-burn measurements. Separate models were run for samples collected from stands burned in the fall, stands burned in the spring, and from the control stand. We used the “anova” function to calculate *F* values and Satterthwaite’s degrees of freedom to determine if time since burning significantly affected each dependent variable (*P* < 0.05; “lmerTest” package; Kuznetsova et al., 2017). If we detected a significant effect of time since burning (*P* < 0.05), then we conducted a Dunnett’s tests to assess which burned timepoints differed from pre-burned measurements (Lenth, 2016). Model residuals were plotted to ensure that they were normally distributed. We used this same approach to assess if ash depth differed between fall and spring burn stands three days after burning.

Prior to running each statistical model, we assessed if there were any outliers using Dixon’s test (Komsta, 2022). Separate tests were conducted for each dependent variable within each season. We detected a

high outlier in POC and bulk C and present results from models run with and without the outlier. Models run without the outlier tended to show a stronger effect of fall burning on POC and bulk C.

3. Results

3.1. Soil C pools: MAOC, POC, and bulk soil C

Prescribed burns in the fall decreased bulk soil C compared to pre-fire measurements (Fig. 1A; $F_{5,15} = 2.8$, $P = 0.05$), but when burns took place in the spring, bulk soil C was instead higher at two years after the burn (Fig. 1B; $F_{5,12} = 2.9$, $P < 0.05$). Specifically, fall-burn bulk soil C decreased by 48 %, from 67.1 ± 6.82 g C kg⁻¹ dry soil (hereafter mean $\pm$ standard error) pre-burn to 35.0 ± 5.17 g C kg⁻¹ dry soil 24 days after the burn ($P = 0.03$; Fig. 1A). Two years after the fall burn, bulk soil C was no longer significantly lower than pre-burned soils ($P = 0.13$). However, when a high outlier measured three days after fall burning was removed from our analysis (Dixon's test, $Q = 0.58$, $P = 0.003$), we detected a 52 % decrease in bulk soil C three days after burning (32.3 ± 8.11 g C kg⁻¹ dry soil, $P = 0.006$) and a 36 % decrease in bulk soil C two years after burning (43.0 ± 7.03 g C kg⁻¹ dry soil, $P = 0.04$). In contrast to fall burning, the spring burn increased bulk soil C from 58.7 ± 10.4 g C kg⁻¹ dry soil before the burn to 96.2 ± 13.8 g C kg⁻¹ dry soil two years after burn ($P < 0.001$; Fig. 1B) and did not change soil C at any other time-point. Bulk soil C did not change over time in the control plot measured at the same time as the fall burn ($F_{5,14} = 0.54$, $P = 0.74$) or at the same time as the spring burn ($F_{3,18} = 0.13$, $P = 0.94$).

Prescribed burns in the fall did not significantly affect POC ($F_{5,18} = 1.07$, $P = 0.41$). However, when the same outlier that was removed from the total bulk soil C analysis was removed from the 3-day post fire sampling event (Dixon's test, $Q = 0.66$, $P < 0.001$), we detected a decrease in POC after fall burning compared to pre-burn measurements ($F_{5,14} = 3.11$, $P = 0.04$; Fig. 1C). Specifically, POC decreased by 61 %, from 36.6 ± 6.97 g C kg⁻¹ dry soil to 14.2 ± 4.78 g C kg⁻¹ dry soil three days after burning ($P = 0.04$), and by 50 % two years after burning (18.3 ± 3.33 g C kg⁻¹ dry soil), although this effect was only significant at $P = 0.07$. In contrast to fall burning, spring burning did not affect POC ($F_{5,15} = 1.32$, $P = 0.31$), averaging 70.2 ± 5.13 g C kg⁻¹ dry soil across all measurements (Fig. 1D). Similarly, POC did not significantly change over time in the control plot measured at the same time as the fall burn ($F_{4,14} = 0.89$, $P = 0.52$) or the spring burn ($F_{1,20} = 0.43$, $P = 0.52$).

Prescribed burns in the fall did not significantly affect MAOC ($F_{5,15} = 2.03$, $P = 0.13$), averaging 11.3 ± 0.66 g C kg⁻¹ dry soil across all timepoints (Fig. 1E). However, MAOC increased over time in the control plot measured at the same time as the fall burn plots ($F_{5,14} = 3.14$, $P = 0.04$), rising from 20.9 ± 2.78 g C kg⁻¹ dry soil before the burn to 29.1 ± 4.23 g C kg⁻¹ dry soil two years after the burn. Unlike fall burning, spring burning increased MAOC over time ($F_{5,12} = 13.0$, $P < 0.001$), rising from 16.2 ± 0.74 g C kg⁻¹ dry soil before burning to 22.1 ± 1.35 g C kg⁻¹ dry soil two years after burning (36 %, Fig. 1F). MAOC measured in the control plot at the same time as the spring burn also increased over time ($F_{5,16} = 4.9$, $P = 0.007$), rising from 20.9 ± 2.78 g C kg⁻¹ dry soil before the burn to 33.5 ± 2.34 g C kg⁻¹ dry soil 2 years after the burn.

PyOM did not significantly change in response to either fall ($F_{5,18} = 1.70$, $P = 0.19$) or spring ($F_{1,12} = 1.28$, $P = 0.33$) burning, averaging 4.41 ± 0.68 g C kg⁻¹ dry soil in plots that were burned in the fall (Figs. 1G) and 5.27 ± 0.93 g C kg⁻¹ dry soil in plots that were burned in the spring (Fig. 1H).

3.2. Microbial respiration

Fall burning increased microbial respiration one month after burning ($F_{5,54} = 54.1$, $P < 0.001$), whereas spring burning decreased microbial respiration compared to pre-burn measurements for over a year ($F_{4,44} = 11.8$, $P < 0.001$; Fig. 2). In response to the fall burn, respiration

increased from 658 ± 97.9 mg C-CO₂ kg⁻¹ dry soil before burning to 1385 ± 250 mg C-CO₂ kg⁻¹ dry soil 24 days after burning ($P = 0.006$) and did not differ from the pre-burn measurement for any other time-point ($P > 0.05$; Fig. 2A). For the spring burn, microbial respiration was consistently lower in all post-burn measurements (363 ± 60.3 mg C-CO₂ kg⁻¹ dry soil 1 year after the fire) compared to the pre-burn measurement (582 ± 72.0 mg C-CO₂ kg⁻¹ dry soil; Fig. 2B). We did not detect a significant change in respiration in the control plot in the fall ($F_{5,10} = 3.14$, $P = 0.06$) or the spring ($F_{4,8} = 3.13$, $P = 0.08$).

3.3. Potential extracellular enzyme activity

Fall burning decreased the potential activity of AG for one year ($F_{5,52} = 3.7$, $P = 0.006$) and decreased BG for one month ($F_{5,55} = 5.4$, $P < 0.001$); both are hydrolytic enzymes involved in C acquisition (Fig. 3). Potential activity of AG decreased from 61.4 ± 6.01 nmol g⁻¹ hr⁻¹ before burning to 27.2 ± 4.13 nmol g⁻¹ hr⁻¹ one year after burning (Fig. 3A), while potential activity of BG decreased from 304 ± 46.0 before burning to 37.3 ± 11.0 nmol g⁻¹ hr⁻¹ 24 days after burning (Fig. 3C). Neither AG ($F_{5,12} = 2.6$, $P = 0.08$) nor BG ($F_{5,7} = 0.91$, $P = 0.52$) potential activity significantly changed over the same time in the control plot. Potential activity of CBH did not change over time in plots burned in the fall ($F_{5,51} = 1.4$, $P = 0.25$) or the control plot ($F_{5,12} = 1.5$, $P = 0.27$; Fig. 3E). In the spring, burning increased AG potential activity three days after burning ($F_{4,52} = 8.1$, $P < 0.001$; Fig. 3B) and CBH potential activity 1.5 years after burning ($F_{4,44} = 3.0$, $P = 0.03$; Fig. 3F), but did not significantly affect BG potential activity ($F_{4,44} = 0.66$, $P = 0.63$; Fig. 3D).

While the potential activity of phenol oxidase—an oxidative enzyme that degrades organic matter—changed over time in plots that were burned in the fall ($F_{5,63} = 4.2$, $P = 0.002$), post-burn activity did not significantly differ from pre-burn activity ($P > 0.05$; Fig. 4A). Spring burning increased potential activity of phenol oxidase six months after the fire ($F_{3,33} = 13$, $P < 0.001$; Fig. 4B). Burning increased potential activity of peroxidase, another oxidative C degrading enzyme, in both the fall ($F_{5,63} = 6.9$, $P < 0.001$; Fig. 4C) and the spring ($F_{4,44} = 24$, $P < 0.001$; Fig. 4D). In the fall, peroxidase potential activity was higher than pre-burn measurements 24 days, six months, and one year after burning; while in the spring, peroxidase potential activity was only higher than pre-burn measurements six months after burning ($P < 0.05$). Peroxidase potential activity decreased over time in the control plot after burning in the fall ($F_{5,5} = 43$, $P < 0.001$) and spring ($F_{4,10} = 42$, $P < 0.001$).

We did not detect a significant effect of fall burning on potential activity of the N-acquiring enzyme NAG ($F_{5,55} = 2.2$, $P = 0.07$; Figure S2A). However, fall burning decreased the potential activity of LAP ($F_{5,54} = 5.5$, $P < 0.001$; Figure S2C), another enzyme involved in N acquisition, as well as PHO ($F_{5,55} = 4.7$, $P = 0.001$; Figure S2E), an enzyme involved in phosphorous acquisition. During this time, neither LAP nor PHO potential activity significantly changed in the control plot ($P > 0.1$). Spring burning did not alter the potential activity of NAG ($F_{4,44} = 0.92$, $P = 0.46$; Figure S2B), LAP ($F_{4,51} = 4.2$, $P = 0.005$; pre-burn potential activity did not significantly differ from post-burn, $P > 0.08$; Figure S2D), or PHO ($F_{4,52} = 0.47$, $P = 0.75$; Figure S2F).

3.4. Ash depth

Average ash depth, our index of burn intensity at the ground surface, trended higher in the fall (1.95 ± 0.40 cm) than in the spring (0.83 ± 0.14 cm), though this difference was only significant at $P = 0.07$ ($F_{1,6} = 4.91$). Moreover, ash depth after the fall burn was more variable than after the spring burn (Fig. 5; $F = 8.59$, $P < 0.001$).

4. Discussion

Expanding the use of prescribed burns is thought to be a critical step

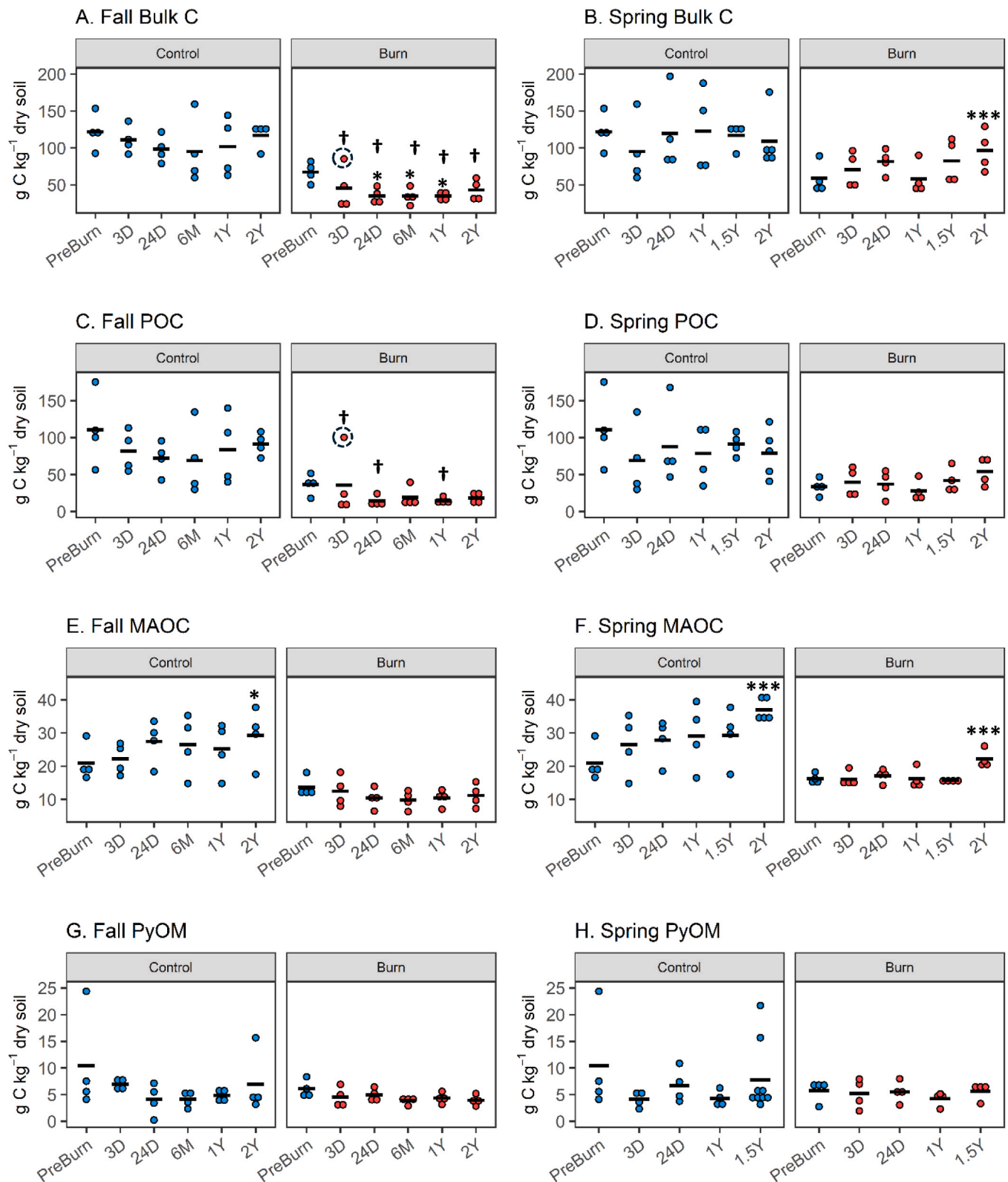


Fig. 1. Soil carbon concentrations in (A, B) total bulk soil, (C, D) POM, (E, F) MAOM, and (G, H) PyOM-C measured after prescribed burns conducted in the fall or spring. Dots correspond to individual measurements, horizontal lines correspond to means, and dot color corresponds to burn status (red = burned and blue = unburned). Asterisks indicate a significant difference between burned and pre-burned measurements (* = $P < 0.05$, ** = $P < 0.01$, *** = $P < 0.001$) as assessed using Dunnett's tests. Crosses also indicate a significant difference between burned and pre-burned measurements when the high outlier in plots A and C (circled) was excluded from analysis ($P < 0.05$ for all).

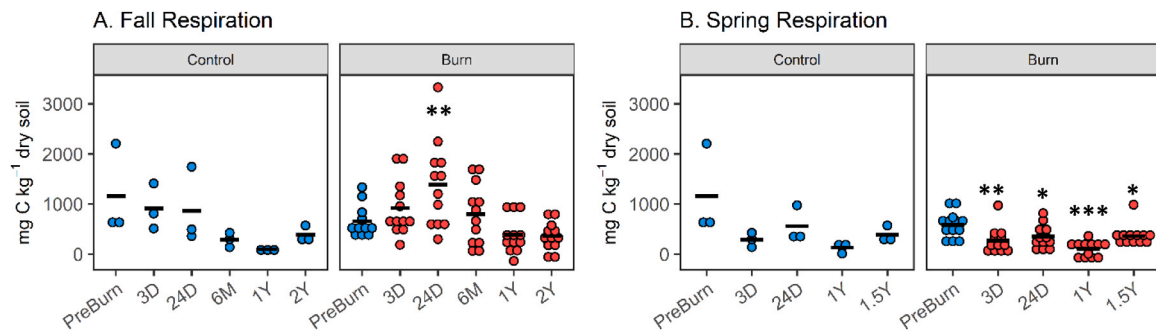


Fig. 2. Microbial respiration measured from soils collected after prescribed burns conducted in the (A) fall or (B) spring. Dots correspond to individual measurements, horizontal lines correspond to means, and dot color corresponds to burn status (red = burned and blue = unburned). Asterisks indicate a significant difference between burned and pre-burned measurements (* = $P < 0.05$, ** = $P < 0.01$, *** = $P < 0.001$) as assessed using Dunnett's tests.

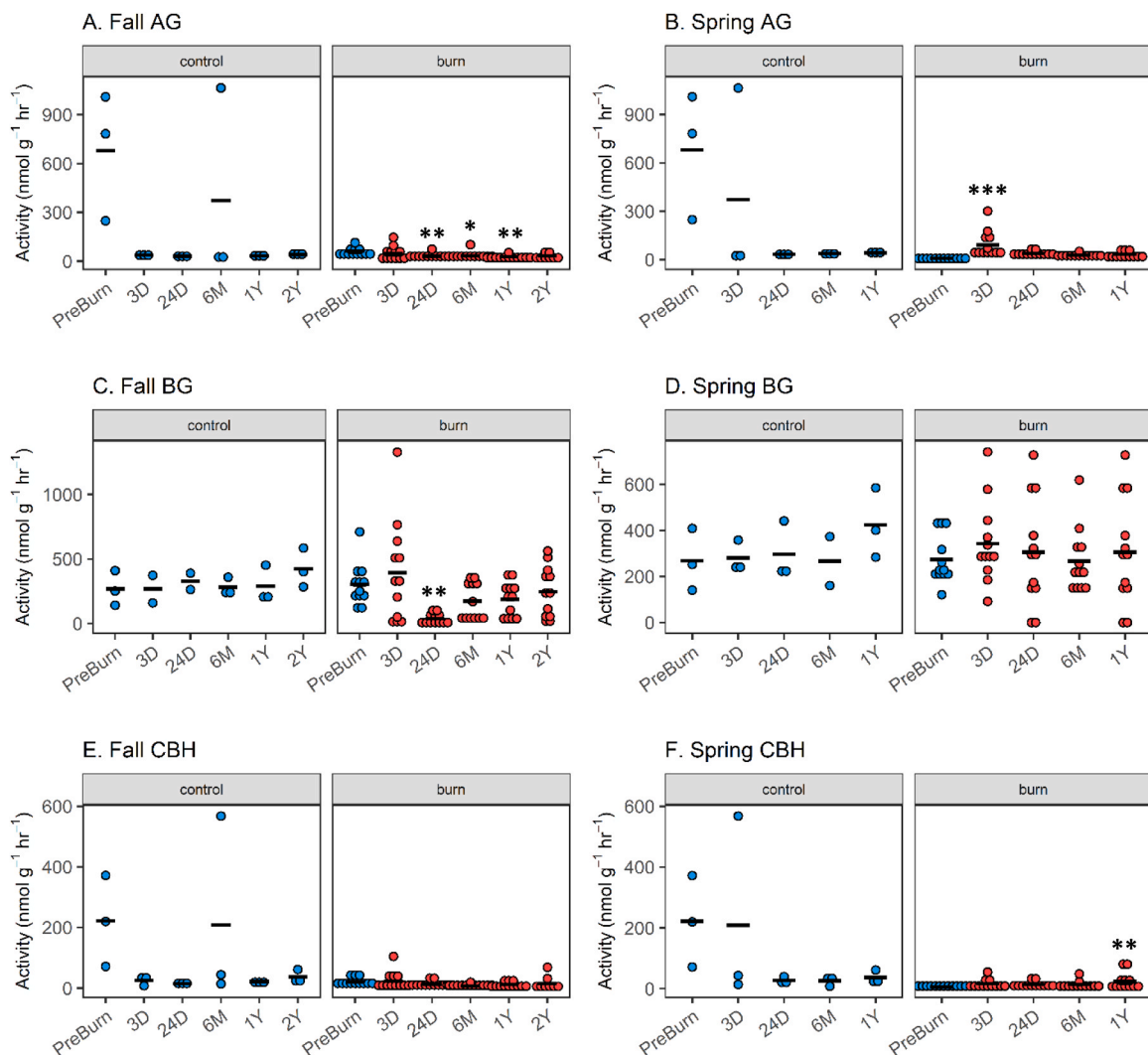


Fig. 3. Potential activity of three hydrolytic C acquiring extracellular enzymes from soils collected after prescribed burns conducted in the (A, C, E) Fall or (B, D, F) Spring. Bars represent means and dots show individual measurements. Color corresponds to burn status (red = burned and blue = unburned). Asterisks indicate a significant difference between burned and pre-burned measurements (* = $P < 0.05$, ** = $P < 0.01$, *** = $P < 0.001$) as assessed using Dunnett's tests.

to slow the proliferation of severe wildfires in young forest stands that are a frequent component of the forested landscape (Jones et al., 2025; Ryan et al., 2013). Yet, it is not clear how burning young forest stands in the spring—outside of historical fire regimes—affects soil C, leading us to monitor surface soil C pools and microbial activity after burning young mixed-conifer forest stands in the fall or spring. In line with our

hypotheses, spring burns did not deplete soil C pools as much as fall burns. Fall burns occurred when soils were drier than in the spring, allowing the fire to burn hotter, resulting in more ash, and combusting more POC. Furthermore, MAOC did not change as much as POC, offering partial support to our hypothesis that MAOC would persist through the burns. Finally, PyOM did not change with prescribed burning in either

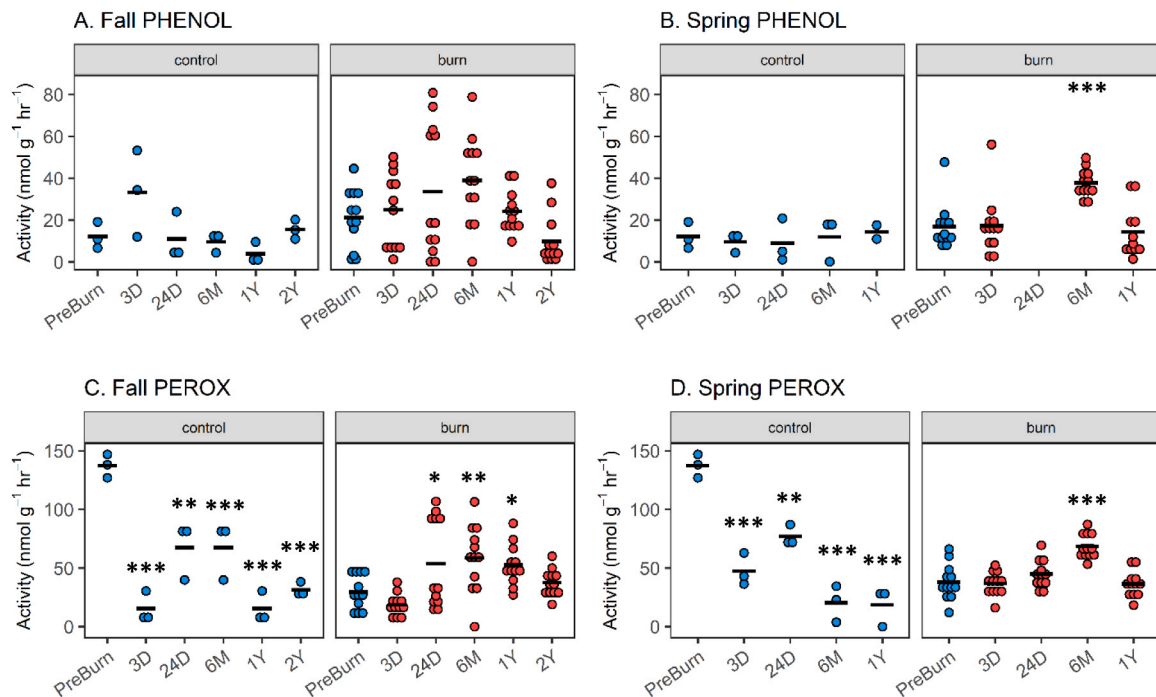


Fig. 4. Activity of two oxidative C degrading extracellular enzymes from soils collected after prescribed burns conducted in the (A, C) Fall or (B, D) Spring. Bars represent mean and dots show individual measurements. Color corresponds to burn status (red = burned and blue = unburned). Asterisks indicate a significant difference between burned and pre-burned measurements (* = $P < 0.05$, ** = $P < 0.01$, *** = $P < 0.001$) as assessed using Dunnett's tests.

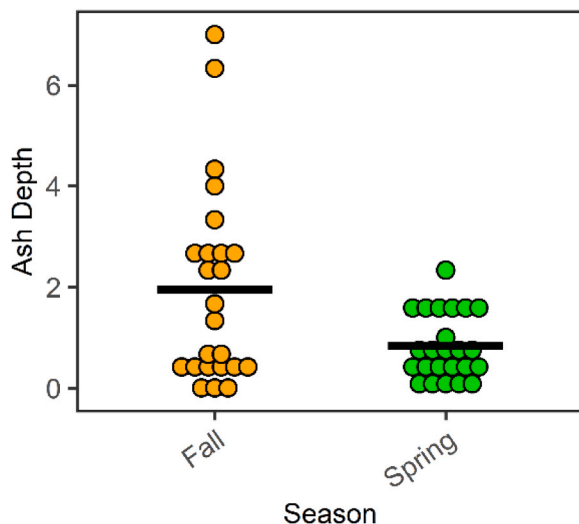


Fig. 5. Ash depth (cm) measured three days after burning stands in either the fall (orange dots) or spring (green dots). Dots correspond to individual measurements and the horizontal black lines represent means.

spring or fall, contrary to our hypothesis that more severe burning would form more PyOM.

Fall burns combusted more organic C in surface soils than spring burns without a concomitant increase in PyOM, depleting soil C. The initial loss of POC and bulk C within days of burning in the fall must have occurred through combustion because, while microbial respiration persisted in burned plots, it could at most decrease bulk C by $\sim 2.8 \text{ g C kg}^{-1}$ at rates measured in the lab, much less than the $> 22 \text{ g C kg}^{-1}$ decrease we observed (compared to the 12 g C kg^{-1} increase in the spring; Fig. 2). Greater C combustion in the fall than the spring suggests that fall burns were more intense. Mean ash depth—an index of soil burn severity—tended to be higher in stands that burned in the fall versus the

spring, and because ash depth was more variable after the fall burn, this suggests that pockets of higher soil burn severity could have combusted more C (Fig. 5), consistent with observations that higher severity prescribed burns can lower soil C (Alcañiz et al., 2018; Fontúrbel et al., 2021). Indeed, these prescribed burns killed small trees (York et al., 2022), suggesting they may have burned hot enough to also combust SOM. Combustion of C during prescribed burns may be more common in soils with a high proportion of POC—which can be more susceptible to combustion (Wang et al., 2023)—consistent with the larger losses of POC than MAOC three days after burning. While the fall burns were hot enough to combust POC, they did not affect soil PyOM-C, contrary to prior findings that prescribed burning can produce PyOM (DeLuca et al., 2020; Fontúrbel et al., 2021; Volkova et al., 2021). The low amount of surface fuels in these young forest stands (York et al., 2022) may not provide enough organic material to be converted to PyOM. If our one-time burn treatment did not pyrolyze much organic matter, then repeated burning over time may be necessary to establish detectable PyOM pools (DeLuca et al., 2020), suggesting that PyOM formation did not immediately offset POC losses to combustion during fall prescribed burns.

In addition to combusting POC, fall burning stimulated microbial respiration in the months after burning, likely due to a pulse of microbial residues or the heat-induced transformation of chemically complex C into more labile C that microorganisms can respire (VanderRoest et al., 2024). Moreover, given the observed decreases in AG, BG, LAP, and PHO potential activity in soils burned in the fall, reduced microbial investment in C, N, and P acquisition suggest high nutrient availability could have also supported the elevated microbial respiration (Allison and Vitousek, 2005). Increased bioavailable C in soils can also prime microbial investment in oxidative enzymes that target more chemically-persistent MAOC (Jilling et al., 2021). Indeed, peroxidase potential activity increased between 24 days and one year after fall burning, potentially keeping MAOC from increasing in fall burn plots despite the observed increase in MAOC in the control plot during this time. As such, respiration by fire-tolerant and/or fast-colonizing soil microorganisms may have decreased bulk C between 3 days and 6

months after fall burning, although this decrease in C was most prominent when the high outlier on day 3 was excluded from the analysis. Even if elevated microbial respiration did not deplete bulk soil C, our results suggest that the persistence of microbial activity can prevent the accumulation of C in the months after fall burning.

Spring burns did not combust as much C as fall burns and did not stimulate microbial respiration, suggesting that wetter conditions limited soil burn severity (Badía et al., 2017). Indeed, neither POC, MAOC, nor PyOM-C decreased after the spring burn, and microbial respiration did not increase, contrary to what we observed after the fall burn. Instead, burning in the spring suppressed microbial respiration for at least 1.5 years. During this time, MAOC increased by 36 % and bulk C increased by 64 %, suggesting that decreased microbial respiration contributed to C accumulation. The suppression of microbial respiration after burning could have resulted from increased microbial mortality if moist spring soils transferred heat more efficiently than drier and warmer fall soils (DeBano, 2000), but spring burning did not induce bacterial or fungal mortality to support this argument (Zhilik, personal communication). Rather, the spring burn may not have been severe enough to produce a pulse in labile C from microbial residues or plant biomass (e.g., root exudates and fine roots) to support microbial respiration (Catalanotti et al., 2018; VanderRoest et al., 2024), helping to explain why microbial respiration was suppressed. We note that fall prescribed burns killed more trees than spring burns (York et al., 2022), perhaps supporting the argument that lower plant residues from dead trees in the spring lowered microbial respiration relative to the fall. Regardless of the mechanisms, our results suggest that spring prescribed burns did not deplete soil C pools, and that suppressed microbial respiration may help explain why C pools increased over two years post fire.

5. Conclusions

We found that prescribed burns in a young mixed-conifer forest in the spring did not deplete surface soil C pools as much as prescribed burns in the fall. In the fall, dry conditions fueled more intense fires that combusted soil POC. Fall prescribed burns also stimulated microbial decomposition in the months following fire, slowing the recovery of soil C pools in young mixed-conifer forests. Bulk surface soil C remained depleted by 50 % for two years, suggesting that conducting prescribed burning at intervals less than two years in young mixed-conifer forests may further deplete soil C. In contrast, prescribed burns in young mixed-conifer forests during the relatively wetter spring season may help keep more C in soils by reducing fire severity and may even increase persistent MAOC pools by over 36 % within the first two years post fire. Taken together, our results suggest that burning young mixed-conifer forest stands in the spring does not adversely affect soil C pools relative to burning in the fall within two years post fire, a positive outcome for forest management efforts aiming to increase burning activity across multiple seasons.

CRediT authorship contribution statement

Robert A. York: Conceptualization, Funding acquisition, Investigation, Methodology, Project administration, Resources, Supervision, Validation, Writing – review & editing. **Jacob Kemner:** Conceptualization, Data curation, Formal analysis, Investigation, Methodology, Writing – review & editing. **Basubi B. Zhilik:** Data curation, Formal analysis, Investigation, Methodology, Writing – review & editing. **Chloe L. Reid:** Data curation, Investigation, Methodology, Writing – review & editing. **Peter M. Homyak:** Conceptualization, Funding acquisition, Investigation, Methodology, Project administration, Resources, Supervision, Writing – review & editing. **Krichels Alexander:** Data curation, Formal analysis, Investigation, Validation, Visualization, Writing – original draft, Methodology, Writing – review & editing. **Sydney I. Glassman:** Conceptualization, Funding acquisition, Investigation,

Methodology, Project administration, Resources, Supervision, Writing – review & editing.

Declaration of Competing Interest

The authors declare no competing interests.

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at [doi:10.1016/j.foreco.2025.123298](https://doi.org/10.1016/j.foreco.2025.123298).

Data availability

All data presented in this manuscript are available in the Dryad Research data repository: <https://doi.org/10.5061/dryad.1zcrjdg5t>.

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