BIOGEOCHEMICAL IMPACTS OF SLASH PILE BURNING IN LODGEPOLE PINE FOREST

A THESIS

Presented to

The Faculty of the Environmental Studies Program

The Colorado College

In Partial Fulfillment of the Requirements for the Degree

Bachelor of Arts in Environmental Science

By

Oliver I. Dunn

May 2021

Dr. Rebecca T. Barnes

Associate Professor of Environmental Science, Colorado College

Dr. Michael J. Wilkins

Associate Professor of Soil and Crop Sciences, Colorado State University

Abstract

Wildfire frequency and severity are increasing as a result of climate change compounded by forest management histories in the Rocky Mountain West. Fire and changes to the disturbance regime alter vegetation, soil biogeochemistry and thus carbon cycling, with the possibility of forcing positive ecosystem feedbacks that further contribute to global climate change. To understand the impacts of pile burning as a management technique and as a proxy for the impacts of severe wildfire, this study analyses a 60-year chronosequence of burn pile scars and surrounding regenerating clear cut Lodgepole pine forest to investigate biogeochemical changes to severely burned soils over time. Soil was characterized and soil incubation experiments were conducted to measure microbial respiration and bioavailability rates. Soils in burn pile scars had less carbon and lower respiration rates compared to regenerating forest soils. Nonlinear recovery of respiration and bioavailability rates, as well as the altered quality of the SOM pool in burn pile soils, suggests that persistent changes to vegetation, soil chemistry, and soil microbial community cause long-term shifts in nutrient cycling and carbon fluxes following burning. Burn pile scars sequester less carbon for more than 60 years after disturbance and may show permanent shifts in ecosystem structure. Used as a proxy for increasing wildfire severity, these results indicate that the Rocky Mountain West is vulnerable to permanent stand structure shifts and a change to becoming a carbon source. Alterations to carbon cycling and ecosystem structure following pile burning and wildfire are essential for land managers to consider in planning for the continued provisioning of ecosystem services.

Acknowledgments

I would like to thank Dr. Rebecca Barnes for being an incredible advisor, mentor, and role model throughout this project and my time at Colorado College. Becca has given unwavering support without which this project would not have been possible, and taught me so much about the research process. Furthermore, through her mentorship she has been a constant source of inspiration for what it means to be a scientist and my place within the field, for which I will be forever grateful.

I also extend my gratitude to lab partners and colleagues Coco Turvold and Michelle Wolford for their support in the lab, workshopping ideas and figures, peer review, and picking up the phone at all hours of the day to answer my questions. It has been a pleasure to work with and learn from each of them.

Thank you to Dr. Mike Wilkins and Amelia Nelson at Colorado State University for their continued collaboration and support, including inspiration in thinking about microbes, Amelia Nelson's assistance in collecting soil samples for us and invaluable feedback and advice from Dr. Mike Wilkins.

Additional thanks for the collaboration of Dr. Chuck Rhoades and Timothy Fegel at the USFS, who generously helped with sample collection and analysis as well as sharing data and expertise that made this project possible.

Table of Contents

Abstract	1
Acknowledgments	2
Introduction	4
Methods	11
Results	16
Discussion	20
Conclusions	28
Figures	29
Works Cited	36

Introduction

In 2020, Colorado experienced three of the largest four wildfires in recorded state history, in a fire season that extended far beyond any historical precedent. These fires had drastic human consequences including loss of lives, homes, and livelihoods, massive evacuations amidst a global pandemic, and smoke choking much of the region (Beradelli 2020). Unfortunately, the link between a changing climate and more extreme fires is clear, and the Rocky Mountain West is particularly at risk (Whitlock *et al.* 2003, Abatzoglou & Williams 2016). Climate-driven disasters like these wildfires, and the harm they cause, are becoming the new norm as records are broken nearly every fire season. Understanding the drivers and consequences of changes in global climate and their links to forest disturbance regimes is critical to mitigate impacts.

The North American continent is an estimated 500 ± 250 million ton sink of carbon per year, but human activity has the potential to alter this balance (U.S. Climate Change Science Program 2007). Forests in the western United States are thought to sequester between 20-40% of all carbon (C) in the contiguous United States, and fire threatens the ability for these systems to store C (Kasischke *et al.* 2013). Anthropogenic disturbances, such as climate change, land conversion, and fire exclusion, have the potential of turning forests in the Rocky Mountain West from carbon sinks into carbon sources by shifting feedbacks in these ecosystems. These changes can result in forests releasing carbon that is currently stored and reducing the ability of ecosystems to uptake more carbon (Houghton & Hackler 2000, Kurz *et al.* 2008). Moreover, fuel buildup from legacies of 20th century land management and fire suppression put these

systems at greater risk of severe wildfire and have the potential to magnify the effects of climate change on changing disturbance regimes (Marlon *et al.* 2012, Higuera *et al.* 2015). However, the potential magnitude and rate of changes in carbon cycling by forests remain unclear, in part because of uncertainty about the impacts changes in disturbance regime will have on soils (Walker *et al.* 2019).

Soils are the largest terrestrial repository of carbon (Crowther *et al.* 2019) and largely regulate the global carbon balance and ecosystem services. This sink plays a critical role in carbon processing, and understanding how such processes will change in the face of climate change provides valuable insight (Boisvenue & Running 2010). For example, biogeochemical processes in soils (e.g., microbial respiration) may illuminate how shifts due to climate change and management solutions can be mitigated and/or managed (Anderson 1992). Because microorganisms play a critical role in both mobilizing and stabilizing carbon inputs, a shift in the balance between these microbial processes towards increased mineralization due to climate change would increase the net carbon flux from soils (Rustad *et al.* 2001, Bond-Lamberty *et al.* 2018, Jansson & Hofmockel 2020).

As managers of more than a third of the land surface in the United States, including more than 50% of carbon stocks in Colorado, federal agencies in this region have significant influence over biogeochemical processes and nutrient cycling through their management practices in public lands (Failey & Dilling 2010, Dilling & Failey 2013). Lands administered by the United States Forest Service (USFS), including the Medicine

Bow Routt National Forest, where our study sites are located, are managed according to multi-use mandates, whose implementation is outlined in forest management plans. Management objectives include maintaining the integrity of soil and air resources, ensuring forest health to provide timber and other extracted products, recreational opportunities, and other multi-use purposes (Public Law 86-517 1960, Medicine Bow National Forest 2003). In addition to land management objectives, such as target stand compositions outlined in the Forest Plan, the USFS is responsible for considering how land management impacts carbon stocks in relation to climate change, including how fire management and logging drive current vegetation trends and alter carbon fluxes (USFS 2013).

Many of the USFS managed forests in Colorado are dominated by Lodgepole pine (*Pinus contorta*), a species of coniferous trees that grow across an estimated 26 million ha of boreal, temperate, and mesothermal climates in the western United States and Canada (Lotan & Perry 1983). Lodgepole pine grows in conjunction with other tree species but is often found in single-aged stands which regenerate through standreplacing disturbances, such as wildfire or logging. Nitrogen and moisture availability are usually the limiting conditions on Lodgepole pine growth (Fahey *et al.* 1985). The distribution, stand structure, and disturbance regime of Lodgepole pine is driven largely by climatic factors (Cwynar & MacDonald 1987, Calder *et al.* 2015) but is also heavily influenced by management practices such as fire suppression and exclusion, controlled burning, clearcutting, selective thinning, and selective replanting of tree species or varieties following logging operations (OECD 2010). Further, because Lodgepole pine is

shade- and competition-intolerant, vegetative succession by shade-tolerant tree species will occur in the absence of a stand-replacing disturbance, in time frames ranging from eighty to several hundred years (Lotan & Perry 1983).

Lodgepole pine is adapted to infrequent but severe stand-replacing fire which allows for regeneration from the seed bank (Baker & Veblen 1990). Historical fire intervals for Lodgepole pine forests range from 150 to 300 years, although most regrowth and carbon sequestration occurs in the first 50 years after disturbance (Kashian *et al.* 2013). Clear cutting of Lodgepole pine forest fulfils a similar ecological role as fire by allowing for forest regeneration. While Lodgepole pine relies on disturbance for regeneration, insufficient time between disturbances because of management practices and climatic conditions pose a threat to the ability of forests to sufficiently regenerate between fires (Turner *et al.* 2019). Although significant research has been conducted on Lodgepole pine forest ecosystems because of their relevance for ecosystem functioning and timber harvest, the impacts of climate change combined with historic and current management regimes raise questions about the future of these forests and their role in carbon cycling.

Pile burning is a longstanding and widespread technique used by land managers such as the USFS to dispose of woody residues, such as those created during clearcutting, and decrease wildfire risk (Zon & Cunningham 1931, Isaac & Hopkins 1937). Woody forest debris is mechanically or manually gathered into piles that land managers burn as a cost effective means of accomplishing management goals such as

fuel load reduction. As disturbances from logging, insect outbreaks, and wildfire increase, pile burning is increasingly used as a management tool in national forests. More than 140,000 burn piles with sizes up to dozens of meters in diameter existed in Northern Colorado alone in the early 2010's (Rhoades *et al.* 2021). Pile burning can create legacies of lasting change to vegetation and biogeochemistry persisting more than five decades after disturbance (Rhoades & Fornwalt 2015).

The increased severity of pile burning creates different impacts than the type of wildfire to which Lodgepole pine ecosystems are adapted. By concentrating fuel load, pile burning creates temperatures that can exceed 700 °C, volatilizing organic matter and altering soil chemistry and mineralogy for elements such as carbon, nitrogen, and phosphorus (Busse *et al.* 2013). This extreme heating can also result in changes to soil hydrology and water retention (Seymour & Tecle 2004). Further, because burning happens in concentrated piles throughout the landscape, pile burning creates a patchwork mosaic of high severity disturbance (Korb *et al.* 2004). Pile burning also often occurs outside of the natural fire season, altering the dynamics of the burn due to differences in weather conditions and soil moisture (Wright *et al.* 2019).

Pile burning leads to both direct and indirect impacts on vegetation recovery and soil biogeochemistry. For example, pile burning can directly affect the soil microbiome due to heat-induced mortality (Pressler *et al.* 2019), as well as result in indirect effects from changes in vegetation, soil chemistry, and SOM pools following fire (Jiménez Esquilín *et al.* 2007). Fire directly impacts vegetation through burning biomass and

destroying the seed bank when sufficient soil temperatures are reached, as they are in burn piles (Beadle 1940, Korb *et al.* 2004). Altered hydrology, soil chemistry, and microbiome functioning persisting after fire also have the potential to alter or prevent vegetation recovery after burn. Because vegetation is the dominant C input to the SOM pool, changes in vegetation due to disturbances such as clear cutting and pile burning have ramifications for the SOM pool, subsequent nutrient cycling, and residence time of carbon in the ecosystem (Litton *et al.* 2004).

Burn piles can be used as a proxy for increased severity wildfire, allowing for control of confounding variables (i.e. treatment history, fuel load, elevation, aspect), which supports the investigation of temporal patterns in C cycling expected following climate-induced changes to fire disturbance regime (Smith et al. 2016). Changes in soil biogeochemistry can provide insights into future ecosystem trajectories. As the climate warms and disturbance regimes change in coniferous forests, there is an increasing possibility of long term shifts in forest stand structure and distribution, or even state shifts to alternate biomes (Emanuel et al. 1985, Coops & Waring 2011, Larson et al. 2013), so using pile burning as a proxy helps to predict changes to nutrient cycling and carbon fluxes. Historical analyses of Lodgepole pine forests found that slight changes in temperature (+0.5°C) during the Medieval Climate Anomaly shifted fire disturbance regimes and feedback cycles, resulting in abrupt ecosystem state shifts (Calder et al. 2015, Calder & Shuman 2017). Using this as a parallel for present day warming, the changes in climatic conditions occurring currently, combined with alterations in feedback cycles, could cause similar drastic shifts in forest stand structure. If this type of shift

were to occur, it would erode ecosystem resilience to continued disturbance, impact the ability of these forests to provide ecosystem services, and shift carbon cycling at the global scale (Thompson 2009, Johnstone *et al.* 2016). Stand replacing forest regeneration after wildfire sequesters carbon released during burning and creates a net zero carbon flux in the long term. However, if a state shift occurs because of altered equilibrium, such as an ecosystems shift resulting in sparser forest stand structures, or a complete shift from forest to grasslands after fire, nutrient cycling would be altered, resulting in a net release of carbon to the atmosphere (Kashian *et al.* 2006). Thus, understanding the potential for ecosystem shifts under current management practices and climatic conditions is critical.

Research Questions

Burn pile scars persist more than 50 years following disturbance (Rhoades and Fornwalt, 2015). However, it remains unclear what factors drive this failure of forest regeneration. Given the importance of soils as a critical link between biogeochemical cycling and ecosystem dynamics, this research seeks to understand how soil characteristics and soil processes shift with time following pile burning and if these shifts mirror the observed changes in vegetation. Because fire directly affects vegetation, soil characteristics, the microbiome, and the relationships between them (Creech *et al.* 2012), soil biogeochemistry is examined to provide insights into these relationships. Previous research indicates that vegetation is different in burn scars compared to surrounding regenerating forest (Rhoades & Fornwalt 2015). We also expect to find changes in the SOM pool, lower soil respiration rates, and changed bioavailability rates

in burn pile soils compared to surrounding regenerating forest because of changes in vegetation, soil chemistry, and soil microbiome, impacting the amount and residence time of carbon in soils. Within the context of changing climate and disturbance regimes, the future trajectory of burn pile scars and associated biogeochemical changes are considered to understand the potential for lasting ecosystem change. Using pile burning as a proxy for severe wildfire, this research will help evaluate the short and long-term effects of increased wildfire frequency and intensity on soil biogeochemistry, with implications for carbon cycling within the context of global climate change.

Methods

Study Site

Study sites were located in the Parks Ranger District of the Medicine Bow-Routt National Forests, in north-central Colorado, USA (Figure 1). The study region has a continental climate with an average elevation of 2900 m, mean annual temperature of 3 °C, and mean annual precipitation of 660 mm (Willow Creek Pass Snotel Site, National Climate Data Center 2012, Natural Resources Conservation Service 2012). Dominant soils types are Typic Cryoboralfs and Typic Cryochrepts (Rhoades & Fornwalt 2015).

Forest stand structure is dominated by Lodgepole pine (*Pinus contorta*). Quaking aspen (*Populus tremuloides*), subalpine fir (*Abies lasiocarpa*) and Engelmann spruce (*Picea engelmannii*) are also present in heterogeneous stands alongside Lodgepole

pine, especially at higher elevations and on northern aspects (Hoffman & Alexander 1980).

In this study area, clear cutting was administered by the USFS in stands of Lodgepole pine dominated forest. Following clear cutting, slash piles of dry woody forest residues from logging were created mechanically and manually, and prescribed burns were performed. This high intensity prescribed burning of slash piles created lasting burn scars characterized by little forest regeneration in comparison to surrounding unburned clear cut forest (Rhoades & Fornwalt 2015). Rhoades and Fornwalt (2015) identified a 50 year chronosequence of prescribed burn piles from the 1960's through the 2000's. Using historical data and aerial photographs, they identified all burn piles in the study area and established sampling plots in five randomly selected burn scars per decade across the chronosequence, controlling for factors such as slope, aspect, and burn scar size (Rhoades & Fornwalt 2015). Because all parts of the study area were clear cut, plots from regenerating forests adjacent to the burn scars can be used as control plots to distinguish between the specific effects of slash pile burning and general clear cut treatment. More detail on site location including climate, soil characteristics, vegetation, and management histories, and chronosequence experimental design is provided by Rhoades and Fornwalt (2015).

Sample Collection

This study used a subset of the plots established by Rhoades and Fornwalt (2015). Mineral soil samples were collected from burn scar plots and adjacent

regenerating forest plots for each of the five decades of the chronosequence in August 2020 by Amelia Nelson (Colorado State University), Chuck Rhoades (USFS), and Timothy Fegel (USFS). Soil samples were collected from the 0-10cm depth using a 7.5 cm bulb core after brushing surface litter and duff away. This subset of samples was maintained as unsieved (i.e. whole) soil samples for soil incubations at Colorado College. Unsieved soil samples were stored at 5 °C until incubation and analyses.

Incubation Experiments

Soil incubation experiments were performed in October and November 2020 at Colorado College. To measure soil respiration and bioavailability rates, incubations were done in triplicate for each whole soil sample. For incubations, approximately 30 grams of unsieved soil, excluding large rocks or organic matter such as roots, was placed in a glass jar (pre-combusted at 500 °C for 5 hours) and left open to the atmosphere at room temperature between incubation time points. At 0, 1-, 3-, 7-, and 14-day time marks, airtight lids were placed on each jar and they were incubated for ~2 hours at room temperature (~22 °C). MilliQ water was added to samples before incubating on days 1, 3, 7 and 14 to return to original mass (day 0) and offset moisture losses due to evaporation. After 2-3 hours of incubation, 10 ml of gas from the jar's headspace was analyzed using the SRI-8610C gas chromatograph (GC). Calibration of the GC was performed using 100 ppm, 1,000 ppm, and 10,000 ppm CO₂ standard gases, and ambient lab air was used to determine the background CO₂ (i.e. the concentration of CO₂ in the jar before the lid was closed) for each incubation. Following

the completion of the 14-day incubation, approximate soil volume for each triplicate was measured using a graduated cylinder.

Elemental Analysis and Isotopic Characterization

For each unsieved soil sample, ~20 grams was dried at 50-60°C for approximately 24 hours and reweighed to obtain soil moisture content gravimetrically. These samples were then ground using a Certiprep 800 Mixer/Mill, and elemental analysis was performed to obtain percent carbon (C) and nitrogen (N) using a CE Elantech at Colorado College. Sample replicates and standards of known carbon and nitrogen concentrations were run for machine calibration (soil reference NC Material 338-400-25, CE Elantech Inc., Lakewood, NJ). Average standard deviation between duplicates was 0.134 and 0.004 for %C and %N respectively, indicating the stability of the instrument.

The unsieved soil samples that were ground and dried for elemental analysis were also analyzed for δ^{13} C and δ^{15} N at the Yale Analytical and Stable Isotopic Center (Yale University, New Haven, CT, USA) in March 2021. Low soil nitrogen concentrations limited accurate δ^{15} N results to a fraction (32%) of samples with higher relative nitrogen amounts.

Another subset of the soil samples collected from the same plots using a 7.5 cm diameter corer with the O horizon removed was processed to remove rocks, mosses, and lichens. These soils were sieved (2 mm) and dried for 48 hours at 60°C by USFS

personnel at the USFS Rocky Mountain Research Station (Fort Collins, CO). These sieved samples were then analyzed for total C and N by dry combustion on a LECO 1000 CHN analyzer (LECO Corporation, St. Joseph, MI, USA). Because more soil samples (i.e., greater sample size per decade) were processed by the USFS, soil nitrogen and carbon analyses from sieved soils are used for all subsequent analysis except bioavailability and respiration rate calculations associated with the whole/unsieved soil samples. Comparison of elemental analyses from sieved and unsieved samples shows these measurements are correlated (average standard deviation of 1.04 and 0.03 for %C and %N, respectively). Given the differences in processing, unsieved samples tended to have a greater fraction of OM.

Data Analysis

Soil respiration and bioavailability rates were calculated for each triplicate, with values (e.g., Figure 2 and 3) representing the average of triplicate incubations. Soil respiration rates were calculated from the change in CO₂ mass in the headspace over each incubation period (starting at ambient lab air concentrations) and normalized to the amount of dry soil in the jar (mg C g⁻¹ soil day⁻¹). To better understand the net result of the microbial community and organic matter quality on carbon residence time in the soil pool, respiration rates were normalized to the amount of carbon in each jar (dry weight soil * %C of whole soil samples) to give a bioavailability rate in terms of mg C g⁻¹ soil C day⁻¹. The percent of soil carbon oxidized over the two-week incubation period was estimated by extrapolating average respiration rates between time points to obtain the amount of carbon respired as a percentage of total available soil carbon.

All statistical analyses were performed using R (version 4.3.3) with p values < 0.05 defining statistical significance. Linear regression was used to find relationships between soil respiration and bioavailability rates and soil characteristics including moisture, elemental composition, isotopic composition, etc. Changes in soil characteristics between treatments over the chronosequence were examined using ANOVA tests and Tukey paired t-tests.

Results

Soil Characteristics

Elemental analysis of sieved soils revealed differences in soil organic matter pools between treatment types and with time since recovery (Figure 2). Burn pile soils 40 years after disturbance had the lowest average carbon content of the chronosequence with mean 3.39 ± 1.1 %C, while regenerating forest soils 20 years after disturbance had the highest average soil carbon with mean 6.73 ± 2.18 %C. Overall, soils from burn piles had a mean of 3.89 ± 1.64 %C, which was significantly lower than that of regenerating forests, with mean 4.81 ± 2.20 %C (p=0.03). Burn pile soils 50 years after disturbance had the lowest nitrogen content of the chronosequence, with mean 0.11 ± 0.05 %N. Regenerating forest 20 years after clear cutting had the highest mean nitrogen content of 0.22 ± 0.05 %. Mean %N was overall slightly higher in regenerating forest than burn pile soils, with means of 0.17 ± 0.07 % and 0.15 ± 0.06 %, respectively. Lowest C:N ratio was found in burn pile soils 20 years after disturbance

with a mean of 23.03 ± 8.02 , while the highest mean C:N ratio of 45.08 ± 10.58 was found in burn pile soils 50 years after disturbance. C:N ratio was not significantly different, overall, between burn piles and regenerating forest, with means of $32.11 \pm$ 10.54 and 33.62 ± 8.01 , respectively. Percent soil moisture varied between treatments and time since disturbance. Highest mean percent soil moisture was in regenerating forests 40 years after disturbance ($4.75 \pm 3.0\%$ H₂O) and lowest in burned soils 20 years after disturbance ($0.91 \pm 0.31\%$ H₂O). Overall, regenerating forest soils tended to have higher soil moisture than burn pile soils, with means of 3.22 ± 2.11 % H₂O and 2.00 ± 1.23 % H₂O, respectively.

Respiration, Bioavailability, and Percent Oxidized

Changes in respiration and bioavailability rates over incubation experiments provide insight into mechanisms impacting organic matter processing. Over the 14-day incubation period, average respiration and bioavailability increased between days 0 to 7 before plateauing after day 7 for the second week of incubation (Figure 3). Significant differences were found between each subsequent time point from day 0 to day 7. No statistical difference was found between day 7 and 14 for average respiration (p=0.112) or bioavailability (p=0.206). Because this trend indicates that day 7 and 14 represent stabilized values for the incubation experiment, averages from these time points are used for all subsequent analysis. Respiration, bioavailability, and oxidation rates are influenced by soil characteristics and disturbance (i.e., treatment) histories. Both respiration and bioavailability rates show large amounts of variability with time since disturbance, although no clear relationship exists for respiration or bioavailability rates (Figure 2). Burn sites had a mean respiration rate of 0.016 ± 0.01 mg C g⁻¹ soil day⁻¹, while regenerating forest had higher mean respiration rates of 0.028 ± 0.02 mg C g⁻¹ soil day⁻¹. Tukey paired t-tests showed these differences to be statistically different (p=0.032). Bioavailability rates were also generally lower in burned soils than regenerating forest soils, with means of 0.45 ± 0.25 mg C g⁻¹ soil C day⁻¹ and 0.64 +/-0.41 mg C g⁻¹ soil C day⁻¹, respectively. However, bioavailability was not statistically different between burn and regenerating forest soils, even when controlling for time since disturbance.

For all soils, respiration rates increased with higher percent soil carbon ($r^2 = 0.289$, p<0.001). When analyzed by treatment type, this relationship was significant for regenerating forest soils ($r^2 = 0.393$, p=0.013) but not for burn pile soils (Figure 4). Respiration was found to significantly increase with higher soil C:N ratio for regenerating forests ($r^2 = 0.746$, p<0.001), but this relationship was not found in burn pile soils (Figure 4). For all soils, respiration increased with increased soil moisture ($r^2 = 0.594$, p<0.001). No significant relationships were found between bioavailability rates and percent carbon, C:N, or soil moisture ratio for burned or regeneration forest (Figure 4).

As expected, the estimated amount of carbon converted from soil organic matter to CO₂ over the two-week experiment (i.e., percent oxidized) and bioavailability rates were found to be positively correlated (r^2 = 0.204, p=0.002). Burned soils had mean 0.687 ± 0.60 %C oxidized, while regenerating forests had a higher mean of 1.041 ± 0.49 %C oxidized. Percent oxidized tended to be lower in soils from burn piles, with a mean of 0.69 ± 0.60 %C oxidized, than regenerating forest soils, with a mean of 1.04 ± 0.49 %C oxidized (t=-1.975, p=0.058). No significant differences in percent oxidized were found between subsequent decades for either burned or regenerating forest soils.

Isotopic Analysis

Information about sources and processing of carbon in soils can be gained from stable isotope analyses of δ^{13} C. Burned and regenerating forest plots had mean δ^{13} C signatures of -25.98 ± 0.68‰ and -25.88 ± 0.48‰, respectively. Regenerating forests 20 years after disturbance had mean δ^{13} C signatures of -25.4 ± 0.22‰ representing the most enriched of the sample groups. Burned soils 40 years post-disturbance were the most depleted, with mean δ^{13} C of -26.37 ± 0.32‰. While δ^{13} C was found to vary between burn and control plots and with time since recovery, this variation was not explained by either of these factors (Figure 3). δ^{13} C generally became less depleted with higher soil %C and higher C:N ratio, although these relationships were not found to be statistically significant. Variation in δ^{13} C was not correlated with respiration rates, bioavailability rates, or % oxidized.

Discussion

Forest management alters vegetation dynamics, soil chemistry, and the soil microbiome, which in turn can force positive feedback loops that influence both vegetative recovery and carbon stocks (Hart *et al.* 2005). Logging practices, and in particular clear cutting, can have long-term (e.g., more than 212 years in coastal forest in British Columbia) and nonlinear effects on ecosystem services (Sutherland 2016). While it is difficult to extrapolate between ecosystems with different vegetation and disturbance intervals, such findings may suggest that long-term and nonlinear effects are possible following clear-cutting (Sass *et al.* 2018). The variation of SOM processing (i.e., respiration and bioavailability rates as shown in Figure 2), with no clear trend over time, aligns with this prediction of complex and persistent impacts following disturbance. Furthermore, the variation in %C, C:N ratio, and isotopic composition (Figure 2) which occurs between subsequent decades in both burn pile soils and regenerating forest soils indicates that there are legacies of the impacts of clearcutting for both treatments.

Changes in vegetation structures from forest to patchy herbaceous understory vegetation after pile burning (Rhoades & Fornwalt 2015) alter soil characteristics and the processing of SOM, and thus have the potential to change soil carbon stocks (Zinke 1962, Guo & Gifford 2002). The volatilization of organic matter during combustion of the soil under burn piles explains the initial loss of the soil carbon, a difference that persists for the entire chronosequence (Figure 2). Because lower soil moisture associated with loss of organic matter reduces respiration in some (Buchmann 2000, Schwendenmann

et al. 2003) but not all ecosystems (Scott-Denton 2003, Cleveland & Townsend 2006, Monson *et al.* 2006, Cleveland *et al.* 2007), the drier soils from the burn piles may contribute to the lower respiration rates observed in burn pile soils. In regenerating forest plots, tree seedling density increases and %C decreases with time since disturbance until the 1980's, when tree seedling density peaks (Rhoades & Fornwalt 2015) and %C reaches a minimum in the 1980's, 40 years after disturbance (Figure 2). These trends indicate that decreases in organic matter over time are associated with forest regeneration. Additionally, such changes may be due to an initial increase in SOM from the incorporation of woody logging debris into the soil of regenerating forests during and following clear cutting operations, which declines over the subsequent decades as these inputs decompose and are not replaced by young seedlings and trees (Cromach *et al.* 1979, Durgin 1980, Jurgensen *et al.* 1997).

While soil carbon in regenerating forest does decrease initially, the simultaneous increase in vegetation biomass demonstrates that carbon sequestration still occurs in these forests (Rhoades & Fornwalt 2015). Soil organic matter in burn pile soils remains lower than regenerating forest soils for all decades and does not vary significantly with time since disturbance, which suggests that inputs from the minimal and patchy revegetation of grasses and understory plants in the decades after disturbance are not replacing SOM lost during clear cutting and pile burning (Rhoades & Fornwalt 2015, Figure 2). The lack of accumulation of soil organic matter over time in burn scars implies that these soils function as a reduced carbon sink compared to that of soils in regenerating forests, a difference which remains more than 60 years after disturbance.

Because litter quality is a primary driver of decomposition rates, the litter from small perennial understory forbs and grasses in burn scars would be expected to have shorter residence times as it accumulates and is more easily processed (Zhang *et al.* 2008). However, bioavailability is generally higher in regenerating forests, indicating the greater variability in burn pile vegetation regeneration affects soil biogeochemistry. Furthermore, litter quality and quantity are not the only driving factors of bioavailability as it is also driven by factors such as microbial community assemblage (Luan *et al.* 2020).

Observed patterns in δ^{13} C-SOM further show the connection between altered vegetation pools and SOM processing. Due to isotope discrimination during photosynthesis, plant tissue is commonly depleted in ¹³C (Farquhar *et al.* 1989) and these differences appear in soil because vegetation is the primary input of ¹³C to soils (Dzurec *et al.* 1985, Tieszen & Boutton 1989). Therefore, the differences in soil ¹³C between treatments (Figure 2) are likely driven by vegetation differences. In addition to varying with environmental conditions, ¹³C signatures are highly species specific (Park & Epstein 1961, Yang *et al.* 2015). Burn pile scars have relatively depleted ¹³C, which may be because SOM is primarily from understory plants, which are generally also depleted in ¹³C in forest ecosystems, compared to more enriched SOM in regenerating forest soils where vegetation input is more so from trees with comparatively enriched ¹³C signatures (van der Merwe & Medina 1991, Bonafini *et al.* 2013).

The δ^{13} C-SOM may also reflect impacts of microbial activity due to preferential degradation and isotopic fractionation during processing, which varies between microbial communities. Still, results from studies are mixed as to whether organic matter decomposition results in fractionation (Blair *et al.* 1985, Cheng 1996, Schweizer *et al.* 1999, Ekblad & Hogberg 2000, Fernandez *et al.* 2003, Boström *et al.* 2007). The enriched signal in forest soils (Figure 2) could be driven in part by a difference in the processing of SOM due to altered microbial function following fire (Hart *et al.* 2005, Pressler *et al.* 2019). Microorganisms are enriched in ¹³C compared to plant material, so given that respiration rates are greater in the regenerating forest soils, one would expect the SOM to be more enriched in regenerating forests, as observed, due to greater microbial respiration (Figure 2, Tieszen & Boutton 1989, Balesdent & Mariotti 1996, Boström *et al.* 2007).

Vegetation changes may also drive the differences in nitrogen availability between treatment types because Lodgepole pine forests are nitrogen limited. For all decades except 50 years after disturbance, regenerating forest soils have a higher mean C:N ratio than burn pile soils (indicating relatively less nitrogen in organic matter), likely due to inputs high in lignin from woody plants versus the more nitrogen-rich OM contributed by the herbaceous cover in burn scars (Figure 2, Boring *et al.* 1988). DIN content is also higher in regenerating forest soils (Rhoades *et al.* 2021) both because there is more nitrogen-rich OM added to the soil but also because higher respiration rates and microbial biomass result in greater rates of nitrogen fixation and mineralization (Fahey *et al.* 1985, Smith *et al.* 2008). Additionally, carbon stored in

plants has a shorter residence time compared to soils, which may create feedback delays in the relationships between vegetation, SOM, and soil chemistry (Yavitt & Fahey 1986).

The direct impact of fire—both organic matter combustion and extreme soil heating—on soil chemistry is another likely mechanism responsible for the persistent changes to carbon stocks and SOM processing. Past research revealed that slash pile burning causes elevated phosphorus and nitrogen concentrations, C:N ratios, and soil pH (Creech et al. 2012). Some of these trends were also found in this study area: burned soils had higher P concentrations and C:N ratios, as well as elevated pH (Rhoades et al. 2021). As the amount of inorganic nitrogen in the soils increased (extractable DIN as reported in Rhoades et al. 2021), the fraction of soil carbon oxidized over the course of the two-week aerobic incubation decreased (this study, Figure 5), suggesting that as more nitrogen is available to microbes in the soil, there is less of a need for them to decompose the SOM for nutrients (Murphy et al. 2017). These results suggest that changes in nitrogen availability following fire within a nitrogen limited ecosystem drive lower respiration in these soils. However, as concluded by Rhoades et al. (2021) and shown by the extensive heterogeneity in soil characteristics found in this study (Figure 2), alterations to soil chemistry alone do not explain the lack of vegetative recovery after fire.

Higher soil pH may be driving (or driven by) changes to SOM processing in burn pile scars. Because soil pH reflects differences in SOM and the interacting relationships

between the microbiome and vegetation with this pool (Fierer 2017), the higher pH found in burn pile soils relative to regenerating forest soils (p=0.008, Rhoades *et al.* 2021) likely reflects multiple ecosystem processes. Lodgepole pine has been found to make soils mildly acidic (Williams et al. 1978), likely driving the lower soil pH found in regenerating forest as compared to burn pile soils (Rhoades et al. 2021). Soil pH was also elevated following pile burning in a different ecosystem (longleaf pine forest in Georgia) and at a shorter time scale (7 years vs. 50 years), which may have captured the initial pulse of phosphorus-driven elevations in pH that is not captured in the decade scale interval of this study (Creech *et al.* 2012). Therefore, changes to soil pH may also be driven by soil chemistry and nutrient changes directly from the fire as well as longer term changes driven by subsequent vegetation dynamics.

Changes in microbial community function, which occur following fire because of direct heat-induced mortality and altered plant community composition (Hart *et al.* 2005), may change SOM processing and carbon stocks. Not only are respiration rates lower in burn pile scars across the 60-year chronosequence, but the drivers of respiration rates appear to be different in burn pile scars than regenerating forests (Figure 4). Soil respiration rates in regenerating forest soils were found to depend on both soil carbon content and C:N ratio, as expected (Schimel *et al.* 1994). However, these relationships were not found in the soils in burn pile scars, meaning that while increased respiration may occur when greater amounts of organic matter is available in regenerating forests, this is not seen in burn scars (Figure 4).

Therefore, differences in the size and composition of the SOM pool alone do not explain the lower respiration rates in pile burn scars. This points to differences in the microbial biomass or functioning of the microbiome. Burn pile soils may have lower overall microbial biomass and different microbial assemblages because of the impacts of fire (Palese et al. 2004, Hart et al. 2005, Busse et al. 2013) and changing vegetation within the Lodgepole pine ecosystem (Baldrian 2016). Although the direct effects of fire are expected to be short lived (Hart et al. 2005), controlled burns have been found to have impacts on microbial communities that extend into the subsoil persisting for more than a decade after disturbance, indicating soil microbial communities are not resilient to fire (Pressler et al. 2019). The functional resilience of the microbial community in Lodgepole pine forests is likely different for pile burning that has a much higher severity but smaller spatial extent than the stand replacing wildfires this ecosystem is adapted to (Botton et al. 2006, Shade et al. 2012). Ongoing research is looking specifically at the microbiome in this study area to understand if changes in microbiome assemblage are responsible for changes in vegetation regeneration, soil respiration, and processing of SOM.

Differences in soils and the processing of the SOM pool persist over the length of the 60-year chronosequence, with even the oldest burned soils dissimilar to the surrounding regenerating forest. Along with altered vegetation patterns and stand structure (Rhoades & Fornwalt 2015), these persisting differences indicate that pile burning creates a legacy of lasting impacts beyond those associated with clear cutting in Lodgepole pine forest. As compared to wildfire, pile burning is known to have more

severe but localized impacts (Busse *et al.* 2013), and the results of this study are consistent with the severe impacts of pile burning found elsewhere (e.g., Creech *et al.* 2012, Switzer *et al.* 2012). The persistence of nonlinear recovery trends in the biogeochemistry and vegetation of the study sites following pile burning is driven by a combination of shifts in vegetation assemblage, microbiome community, and soil chemistry. However, none of these drivers fully explain the persistence of disturbance impacts.

Chronosequence study design, while a valuable tool for evaluating long term changes, has limitations that may obscure mechanisms and thus restrict conclusions. Following disturbance of Lodgepole pine forests, variations in stand structure can persist that take up to 200 years to converge to a homogeneous state (Kashian *et al.* 2005), so the 60 year chronosequence used in this study may be insufficient to see the expected stand recovery. While chronosequence study design assumes convergent successional trajectories and repeating temporal patterns (Walker *et al.* 2010), we observed nonlinear recovery and know that changes in climate and forest ecology have occurred over the 60 year chronosequence (Chhin *et al.* 2008, Pelz & Smith 2012). The impacts of this variation in regeneration temporally are unclear, and more time may be needed to see vegetation and soil biogeochemistry return to pre-fire conditions.

Another distinct possibility is that pile burning has permanently shifted forest stand structure and soil characteristics, and vegetative regeneration will not occur given current climate trends. Non-linear recovery after pile burning suggests the possibility

that sufficient disturbance altered the stability of the system, resulting in permanent stand structure shifts (Graham 2021, Pingree & Kobziar 2019). The majority of seedling establishment for regenerating Lodgepole pine forests is expected to occur within the first 10 years after fire (Stevens-Rumann *et al.* 2018), so the lack of seedling establishment 60 years after fire (Rhoades *et al.* 2021), along with the competition from established understory native plant communities in burn scars, suggests that Lodgepole regeneration is unlikely.

Conclusions

The effects of pile burning on soil biogeochemistry provide insights into the potential for disturbances to compound the results of climate-induced changes, making Lodgepole pine forests more vulnerable to disturbance and permanent shifts in forest structure (Figure 6, Stevens-Rumann *et al.* 2018). Climatic variation has been found to drive dominant vegetation and disturbance patterns, with small increases in temperature historically causing significant shifts in fire regime on this landscape (Calder *et al.* 2015). These changes in disturbance regime because of climate change can result in rapid state shifts of the ecosystem structure (Calder & Shuman 2017). As the climate warms, the regeneration of Lodgepole pine may be threatened by disturbances (Turner *et al.* 2019). The impacts of Lodgepole pine regeneration failure can be predicted by using pile burning as an extreme example of the potential effects of more frequent and severe fires in a warmer and drier climate. While the abrupt change of ecosystem structure resulting from pile burning is most visible in vegetation patterns, biogeochemical state

changes accompany it, resulting in long term changes to carbon and nutrient processing (McLauchlan *et al.* 2014).

Perhaps most significantly, both the soils and vegetation in burn pile scars are sequestering less carbon. If similar patterns occur in these ecosystems on a larger spatial scale following wildfires (which are becoming more frequent and severe), such a loss of carbon sequestration would contribute significantly to positive feedback loops that exacerbate climate change (Figure 6, Rocca *et al.* 2014, IPCC 2018). As land managers seek to promote ecosystem resilience to ensure the continuation of ecosystem services, the impacts of pile burning on long-term forest stand structure, carbon sequestration, and likelihood of catastrophic wildfire must be considered as an indicator in the context of already shifting climatic conditions.

Figures

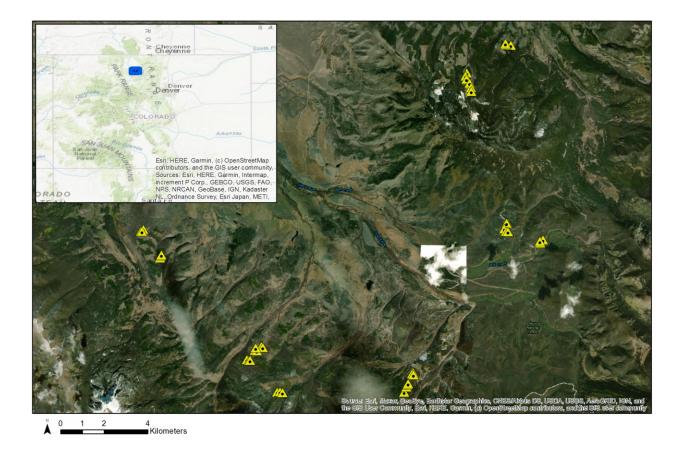


Figure 1: Map of study plot locations represented by yellow triangles, in the Medicine Bow-Routt National Forest, Colorado, USA (extent indicated by blue rectangle, upper left insert). Site locations from Rhoades and Fornwalt (2015).

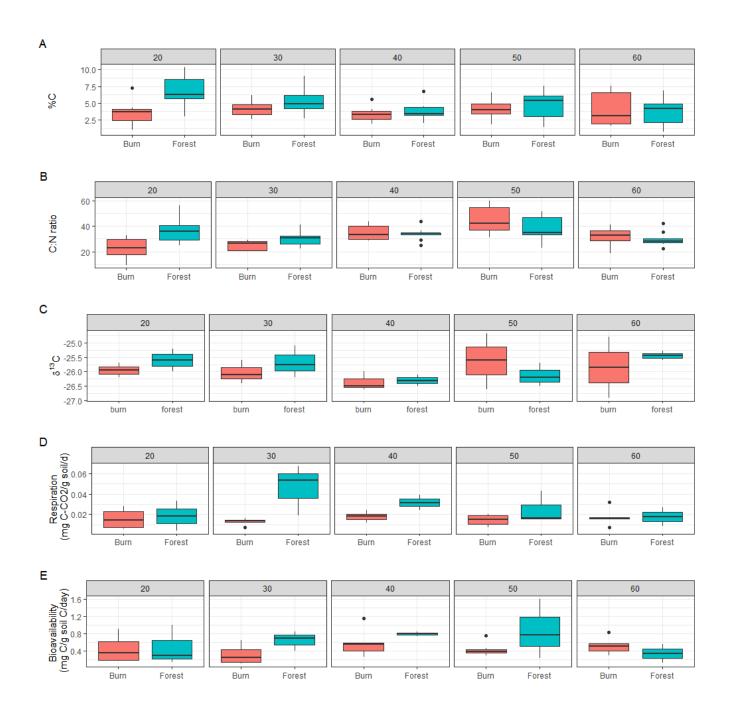


Figure 2: Soil %C, C:N ratio, δ^{13} C, average respiration rate, and average bioavailability rate by years since disturbance for burn piles and regenerating forests. Soil C and C:N ratio tends to be higher in burned soils. Regenerating forest generally had more enriched ¹³C signatures, except 50 years after disturbance; although no significant difference was found between burn and control plots in any decade. Respiration rates generally peak 30 years after disturbance then decreases with time in regenerating forest, while not varying in burn piles over time. Bioavailability rates vary with time since disturbance and between treatments with no clear trend present.

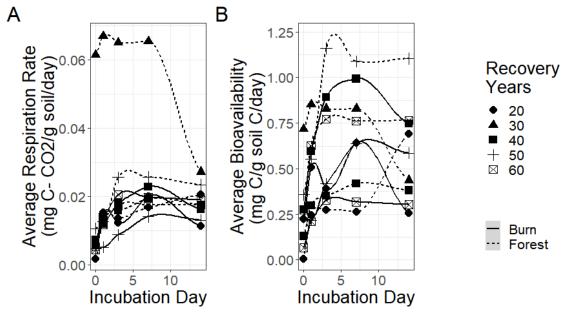


Figure 3: Average respiration rate (A) and bioavailability rate (B) across the 14 day incubation time series for burn and control plots by decade, with treatment represented by line type and years since disturbance represented by shape. While variation exists, the general trend is of initially increasing respiration and bioavailability rates before plateauing for the second week of the incubation period.

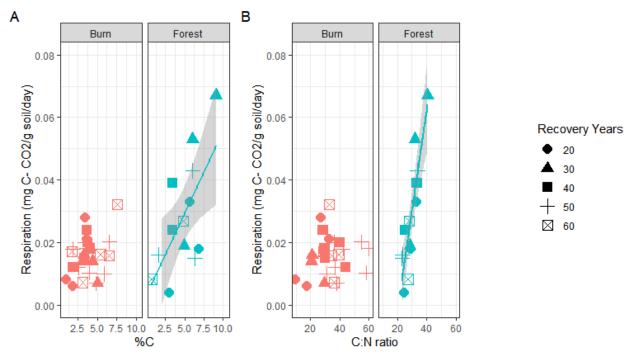


Figure 4: Average respiration rate against percent soil carbon (A) and soil C:N ratio (B) by burn plots and regenerating forest, with years since disturbance represented by shape.

In regenerating forests, respiration rate is correlated with percent soil carbon (r^2 =0.393, p=0.013) and C:N ratio (r^2 =0.746, p<0.001), represented by lines of best fit with 95% confidence intervals. No significant relationships were found between respiration rate and %C or C:N ratio in burned soils. No clear trends exist with years since disturbance for either treatment.

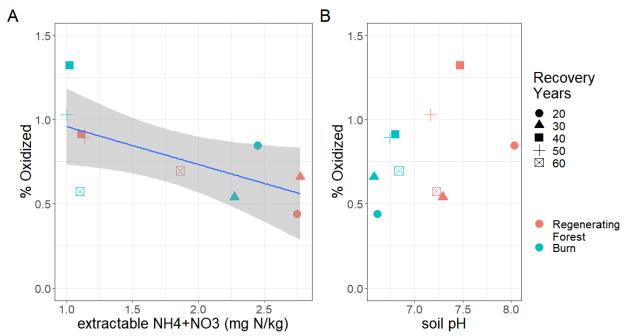


Figure 5: Percent oxidized against average DIN with line of best fit and 95% confidence interval (A) and against soil pH (B) (Rhoades *et al.* 2021), with recovery time represented by shape and treatment type by color. Increased DIN is correlated with decreased fraction oxidized (r^2 =0.339 p=0.045). Regenerating forest soils have higher soil pH than burn piles (p=0.008) but is not correlated with percent oxidized.

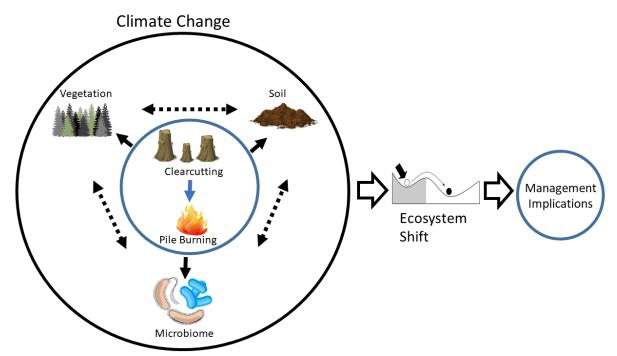


Figure 6: Conceptual diagram of the relationship between management practices and ecosystem processes within the context of climate change, with implications for ecosystem shifts all informing management decisions. Clear cutting and subsequent pile burning creates lasting changes to vegetation, soil properties, and microbial functioning. These changes affect the relationships between vegetation and microbiome (i.e., Beck et al. 2020), vegetation and soil characteristics (i.e., Stohlgren & Bachand 1997, Griffin et al. 2011), and soil characteristics and microbiome (i.e., Fierer 2017). Alterations in these relationships create feedback cycles shifting carbon cycling with implications for global climate change (IPCC 2018). By using pile burning as a proxy for the impacts of increased wildfire severity, these changes provide insights into future changes possible with climate change in the Rocky Mountain West, and the potential for permanent ecosystem shift (Kurz et al. 2008, Stevens-Rumann et al. 2018). Land managers such as the USFS can use these findings to better achieve goals of carbon sequestration, ecosystem resilience, and the continued provision of ecosystem services (Buma & Wessman 2013). Ecosystem shift sub-diagram adapted from Biggs et al. (2012).

Works Cited

Abatzoglou, J. T., and A. P. Williams. 2016. Impact of anthropogenic climate change on wildfire across western US forests. Proc. Natl. Acad. Sci. 113: 11770–11775.

Anderson, J. M. 1992. Responses of Soils to Climate Change. *In* Advances in Ecological Research. pp. 163–210, Elsevier. Available at: https://linkinghub.elsevier.com/retrieve/pii/S0065250408601361 [Accessed March 23, 2021].

- Baker, W. L., and T. T. Veblen. 1990. Spruce Beetles and Fires in the Nineteenth-Century Subalpine Forests of Western Colorado, U.S.A. Arct. Alp. Res. 22: 65.
- Baldrian, P. 2016. Forest microbiome: diversity, complexity and dynamics E. Banin (Ed.). FEMS Microbiol. Rev. fuw040.
- Balesdent, J., and A. Mariotti. 1996. Measurement of soil organic matter turnover using 13C natural abundance.
- Beadle, N. C. W. 1940. Soil Temperatures During Forest Fires and Their Effect on the Survival of Vegetation. J. Ecol. 28: 180.
- Beck, J. L., J. A. Cale, J. C. Rodriguez-Ramos, S. S. Kanekar, J. Karst, J. F. Cahill, S. W. Simard, and N. Erbilgin. 2020. Changes in soil fungal communities following anthropogenic disturbance are linked to decreased lodgepole pine seedling performance E. Wandrag (Ed.). J. Appl. Ecol. 57: 1292–1302.
- Beradelli, J. 2020. Colorado's record-breaking wildfires show "climate change is here and now." CBS News. Available at: https://www.cbsnews.com/news/coloradowildfire-climate-change-evacuations-grand-county/.
- Biggs, R., C. Bleckner, C. Folke, L. J. Gordon, M. Norstrom, M. Nystrom, and G. D. Peterson. 2012. Regime Shifts. Encylocpedia Theor. Ecol. Univ. Calif. Press.
- Blair, N., A. Leu, E. Muñoz, J. Olsen, E. Kwong, and D. Des Marais. 1985. Carbon isotopic fractionation in heterotrophic microbial metabolism. Appl. Environ. Microbiol. 50: 996–1001.
- Boisvenue, C., and S. W. Running. 2010. Simulations show decreasing carbon stocks and potential for carbon emissions in Rocky Mountain forests over the next century. Ecol. Appl. 20: 1302–1319.
- Bonafini, M., M. Pellegrini, P. Ditchfield, and A. M. Pollard. 2013. Investigation of the 'canopy effect' in the isotope ecology of temperate woodlands. J. Archaeol. Sci. 40: 3926–3935.
- Bond-Lamberty, B., V. L. Bailey, M. Chen, C. M. Gough, and R. Vargas. 2018. Globally rising soil heterotrophic respiration over recent decades. Nature 560: 80–83.
- Boring, LindsayR., WayneT. Swank, JackB. Waide, and GrayS. Henderson. 1988. Sources, fates, and impacts of nitrogen inputs to terrestrial ecosystems: review and synthesis. Biogeochemistry 6. Available at: http://link.springer.com/10.1007/BF00003034 [Accessed March 18, 2021].
- Boström, B., D. Comstedt, and A. Ekblad. 2007. Isotope fractionation and 13C enrichment in soil profiles during the decomposition of soil organic matter. Oecologia 153: 89–98.
- Botton, S., M. van Heusden, J. R. Parsons, H. Smidt, and N. van Straalen. 2006. Resilience of Microbial Systems Towards Disturbances. Crit. Rev. Microbiol. 32: 101–112.

- Buchmann, N. 2000. Biotic and abiotic factors controlling soil respiration rates in Picea abies stands. Soil Biol. Biochem. 32: 1625–1635.
- Buma, B., and C. A. Wessman. 2013. Forest resilience, climate change, and opportunities for adaptation: A specific case of a general problem. For. Ecol. Manag. 306: 216–225.
- Busse, M. D., C. J. Shestak, and K. R. Hubbert. 2013. Soil heating during burning of forest slash piles and wood piles. Int. J. Wildland Fire 22: 786.
- Calder, W. J., D. Parker, C. J. Stopka, G. Jiménez-Moreno, and B. N. Shuman. 2015. Medieval warming initiated exceptionally large wildfire outbreaks in the Rocky Mountains. Proc. Natl. Acad. Sci. 112: 13261–13266.
- Calder, W. J., and B. Shuman. 2017. Extensive wildfires, climate change, and an abrupt state change in subalpine ribbon forests, Colorado. Ecology 98: 2585–2600.
- Cheng, W. 1996. Measurement of rhizosphere respiration and organic matter decomposition using natural 13C. Plant Soil 183: 263–268.
- Chhin, S., E. H. (Ted) Hogg, V. J. Lieffers, and S. Huang. 2008. Potential effects of climate change on the growth of lodgepole pine across diameter size classes and ecological regions. For. Ecol. Manag. 256: 1692–1703.
- Cleveland, C. C., D. R. Nemergut, S. K. Schmidt, and A. R. Townsend. 2007. Increases in soil respiration following labile carbon additions linked to rapid shifts in soil microbial community composition. Biogeochemistry 82: 229–240.
- Cleveland, C. C., and A. R. Townsend. 2006. Nutrient additions to a tropical rain forest drive substantial soil carbon dioxide losses to the atmosphere. Proc. Natl. Acad. Sci. 103: 10316–10321.
- Coops, N. C., and R. H. Waring. 2011. A process-based approach to estimate lodgepole pine (Pinus contorta Dougl.) distribution in the Pacific Northwest under climate change. Clim. Change 105: 313–328.
- Creech, M. N., L. Katherine Kirkman, and L. A. Morris. 2012. Alteration and Recovery of Slash Pile Burn Sites in the Restoration of a Fire-Maintained Ecosystem. Restor. Ecol. 20: 505–516.
- Cromach, K., F. J. Swahson, and C. C. Grier. 1979. A comparison of harvesting methods and their impact on soils and environment in the Pacific Northwest.
- Crowther, T. W., J. van den Hoogen, J. Wan, M. A. Mayes, A. D. Keiser, L. Mo, C. Averill, and D. S. Maynard. 2019. The global soil community and its influence on biogeochemistry. Science 365: eaav0550.
- Cwynar, L. C., and G. M. MacDonald. 1987. Geographical Variation of Lodgepole Pine in Relation to Population History. Am. Nat. 129: 463–469.
- Dilling, L., and E. Failey. 2013. Managing carbon in a multiple use world: The implications of land-use decision context for carbon management. Glob. Environ. Change 23: 291–300.
- Durgin, P. B. 1980. Organic matter content of soil after logging of fir and redwood forests. U.S. Department of Agriculture, Forest Service, Pacific Southwest Forest and Range Experiment Station, Berkeley, CA Available at: https://www.fs.usda.gov/treesearch/pubs/6902 [Accessed March 26, 2021].
- Dzurec, R. S., T. W. Boutton, M. M. Caldwell, and B. N. Smith. 1985. Carbon isotope ratios of soil organic matter and their use in assessing community composition changes in Curlew Valley, Utah. Oecologia 66: 17–24.

- Ekblad, A., and P. Hogberg. 2000. Analysis of d13C of CO2 distinguishes between microbial respiration of added C4-sucrose and other soil respiration in a C3-ecosystem.
- Emanuel, W. R., H. H. Shugart, and M. P. Stevenson. 1985. Climatic change and the broad-scale distribution of terrestrial ecosystem complexes. Clim. Change 7: 29–43.
- Fahey, T. J., J. B. Yavitt, J. A. Pearson, and D. H. Knight. 1985. The nitrogen cycle in lodgepole pine forests, southeastern Wyoming. Biogeochemistry 1: 257–275.
- Failey, E. L., and L. Dilling. 2010. Carbon stewardship: land management decisions and the potential for carbon sequestration in Colorado, USA. Environ. Res. Lett. 5: 024005.
- Farquhar, G. D., J. R. Ehleringer, and K. T. Hubick. 1989. Carbon Isotope Discrimination and Photosynthesis. Annu. Rev. Plant Physiol. Plant Mol. Biol. 40: 503–537.
- Fernandez, I., N. Mahieu, and G. Cadisch. 2003. Carbon isotopic fractionation during decomposition of plant materials of different quality. Glob. Biogeochem. Cycles 17: n/a-n/a.
- Fierer, N. 2017. Embracing the unknown: disentangling the complexities of the soil microbiome. Nat. Rev. Microbiol. 15: 579–590.
- Griffin, J. M., M. G. Turner, and M. Simard. 2011. Nitrogen cycling following mountain pine beetle disturbance in lodgepole pine forests of Greater Yellowstone. For. Ecol. Manag. 261: 1077–1089.
- Guo, L. B., and R. M. Gifford. 2002. Soil carbon stocks and land use change: a meta analysis: Soil Carbon Stocks and Land Use Change. Glob. Change Biol. 8: 345–360.
- Hart, S. C., T. H. DeLuca, G. S. Newman, M. D. MacKenzie, and S. I. Boyle. 2005. Post-fire vegetative dynamics as drivers of microbial community structure and function in forest soils. For. Ecol. Manag. 220: 166–184.
- Higuera, P. E., J. T. Abatzoglou, J. S. Littell, and P. Morgan. 2015. The Changing Strength and Nature of Fire-Climate Relationships in the Northern Rocky Mountains, U.S.A., 1902-2008 C. Carcaillet (Ed.). PLOS ONE 10: e0127563.
- Hoffman, G. R., and R. R. Alexander. 1980. Forest vegetation of the Routt National Forest in northwestern Colorado: a habitat type classification. Aspen Bibliogr. Pap. 4549 45.
- Houghton, R. A., and J. L. Hackler. 2000. Changes in terrestrial carbon storage in the United States. 1: The roles of agriculture and forestry: *Carbon storage in the* U.S.A.: agriculture and forestry. Glob. Ecol. Biogeogr. 9: 125–144.
- IPCC. 2018. : Global Warming of 1.5°C.An IPCC Special Report on the impacts of global warming of 1.5°C above pre-industrial levels and related global greenhouse gas emission pathways, in the context of strengthening the global response to the threat of climate change, sustainable development, and efforts to eradicate poverty.
- Isaac, L. A., and H. G. Hopkins. 1937. The Forest Soil of the Douglas Fir Region, and Changes Wrought Upon it by Logging and Slash Burning. Ecology 18: 264–279.
- Jansson, J. K., and K. S. Hofmockel. 2020. Soil microbiomes and climate change. Nat. Rev. Microbiol. 18: 35–46.

- Jiménez Esquilín, A. E., M. E. Stromberger, W. J. Massman, J. M. Frank, and W. D. Shepperd. 2007. Microbial community structure and activity in a Colorado Rocky Mountain forest soil scarred by slash pile burning. Soil Biol. Biochem. 39: 1111–1120.
- Johnstone, J. F., C. D. Allen, J. F. Franklin, L. E. Frelich, B. J. Harvey, P. E. Higuera, M. C. Mack, R. K. Meentemeyer, M. R. Metz, G. L. Perry, T. Schoennagel, and M. G. Turner. 2016. Changing disturbance regimes, ecological memory, and forest resilience. Front. Ecol. Environ. 14: 369–378.
- Jurgensen, M. F., A. E. Harvey, R. T. Graham, D. S. Page-Dumroese, J. R. Tonn, M. J. Larsen, and T. B. Jain. 1997. Impacts of Timber Harvesting on Soil Organic Matter, Nitrogen, Productivity,. For. Sctence 43: 18.
- Kashian, D. M., W. H. Romme, D. B. Tinker, M. G. Turner, and M. G. Ryan. 2006. Carbon Storage on Landscapes with Stand-replacing Fires. BioScience 56: 598.
- Kashian, D. M., W. H. Romme, D. B. Tinker, M. G. Turner, and M. G. Ryan. 2013. Postfire changes in forest carbon storage over a 300-year chronosequence of *Pinus contorta* -dominated forests. Ecol. Monogr. 83: 49–66.
- Kashian, D. M., M. G. Turner, and W. H. Romme. 2005. Variability in Leaf Area and Stemwood Increment Along a 300-year Lodgepole Pine Chronosequence. Ecosystems 8: 48–61.
- Kasischke, E. S., B. D. Amiro, N. N. Barger, N. H. F. French, S. J. Goetz, G. Grosse, M. E. Harmon, J. A. Hicke, S. Liu, and J. G. Masek. 2013. Impacts of disturbance on the terrestrial carbon budget of North America: Disturbance and Carbon Cycling. J. Geophys. Res. Biogeosciences 118: 303–316.
- Korb, J. E., N. C. Johnson, and W. W. Covington. 2004. Slash Pile Burning Effects on Soil Biotic and Chemical Properties and Plant Establishment: Recommendations for Amelioration. Restor. Ecol. 12: 52–62.
- Kurz, W. A., C. C. Dymond, G. Stinson, G. J. Rampley, E. T. Neilson, A. L. Carroll, T. Ebata, and L. Safranyik. 2008. Mountain pine beetle and forest carbon feedback to climate change. Nature 452: 987–990.
- Larson, A. J., R. T. Belote, C. A. Cansler, S. A. Parks, and M. S. Dietz. 2013. Latent resilience in ponderosa pine forest: effects of resumed frequent fire. Ecol. Appl. 23: 1243–1249.
- Litton, C. M., M. G. Ryan, and D. H. Knight. 2004. Effects of Tree Density and Stand Age on Carbon Allocation Patters in Post-fire Lodgepole Pine. Ecol. Appl. 14: 460–475.
- Lotan, J. E., and D. A. Perry. 1983. Ecology and regeneration of lodgepole pine. In: agricultural Handbook No. 606.
- Luan, L., C. Liang, L. Chen, H. Wang, Q. Xu, Y. Jiang, and B. Sun. 2020. Coupling Bacterial Community Assembly to Microbial Metabolism across Soil Profiles N. Bouskill (Ed.). mSystems 5: e00298-20, /msystems/5/3/msys.00298-20.atom.
- Marlon, J. R., P. J. Bartlein, D. G. Gavin, C. J. Long, R. S. Anderson, C. E. Briles, K. J. Brown, D. Colombaroli, D. J. Hallett, M. J. Power, E. A. Scharf, and M. K. Walsh. 2012. Long-term perspective on wildfires in the western USA. Proc. Natl. Acad. Sci. 109: E535–E543.
- McLauchlan, K. K. et al. 2014. Reconstructing Disturbances and Their Biogeochemical Consequences over Multiple Timescales. BioScience 64: 105–116.

Medicine Bow National Forest. 2003. Revised Land and Resource Management Plan. Available at:

https://www.fs.usda.gov/detail/mbr/landmanagement/planning/?cid=fsbdev3_025 109.

- van der Merwe, N. J., and E. Medina. 1991. The canopy effect, carbon isotope ratios and foodwebs in amazonia. J. Archaeol. Sci. 18: 249–259.
- Monson, R. K., D. L. Lipson, S. P. Burns, A. A. Turnipseed, A. C. Delany, M. W. Williams, and S. K. Schmidt. 2006. Winter forest soil respiration controlled by climate and microbial community composition. Nature 439: 711–714.
- Murphy, C. J., E. M. Baggs, N. Morley, D. P. Wall, and E. Paterson. 2017. Nitrogen availability alters rhizosphere processes mediating soil organic matter mineralisation. Plant Soil 417: 499–510.
- National Climate Data Center. 2012. Walden, CO Site: 058756 194892005.
- Natural Resources Conservation Service. 2012. National Water and Climate Center, SNOTEL Site Willow Creek Pass (869); 1981-2010 annual total precipitation data.
- OECD. 2010. "Section 5 Lodgepole pine (Pinus contorta)", in Safety Assessment of Transgenic Organisms, Volume 3: OECD Consensus Documents, OECD Publishing, Paris.
- Palese, A. M., G. Giovannini, S. Lucchesi, S. Dumontet, and P. Perucci. 2004. Effect of fire on soil C, N and microbial biomass. Agronomie 24: 47–53.
- Park, R., and S. Epstein. 1961. Metabolic fractionation of C13 & C12 in plants.
- Pelz, K. A., and F. W. Smith. 2012. Thirty year change in lodgepole and lodgepole/mixed conifer forest structure following 1980s mountain pine beetle outbreak in western Colorado, USA. For. Ecol. Manag. 280: 93–102.
- Pingree, M. R. A., and L. N. Kobziar. 2019. The myth of the biological threshold: A review of biological responses to soil heating associated with wildland fire. For. Ecol. Manag. 432: 1022–1029.
- Pressler, Y., J. C. Moore, and M. F. Cotrufo. 2019. Belowground community responses to fire: meta-analysis reveals contrasting responses of soil microorganisms and mesofauna. Oikos 128: 309–327.
- Public Law 86-517. 1960. Multiple-use Sustained-yield Act of 1960.
- Rhoades, C. C., T. S. Fegel, T. Zaman, P. J. Fornwalt, and S. P. Miller. 2021. Are Soil Changes Responsible for Persistent Slash Pile Burn Scars in Lodgepole Pine Forests?
- Rhoades, C. C., and P. J. Fornwalt. 2015. Pile burning creates a fifty-year legacy of openings in regenerating lodgepole pine forests in Colorado. For. Ecol. Manag. 336: 203–209.
- Rocca, M. E., P. M. Brown, L. H. MacDonald, and C. M. Carrico. 2014. Climate change impacts on fire regimes and key ecosystem services in Rocky Mountain forests. For. Ecol. Manag. 327: 290–305.
- Rustad, L., J. Campbell, G. Marion, R. Norby, M. Mitchell, A. Hartley, J. Cornelissen, and J. Gurevitch. 2001. A meta-analysis of the response of soil respiration, net nitrogen mineralization, and aboveground plant growth to experimental ecosystem warming. Oecologia 126: 543–562.
- Sass, E. M., A. W. D'Amato, and D. R. Foster. 2018. Lasting legacies of historical

clearcutting, wind, and salvage logging on old-growth Tsuga canadensis-Pinus strobus forests. For. Ecol. Manag. 419–420: 31–41.

- Schimel, D. S., B. H. Braswell, E. A. Holland, R. McKeown, D. S. Ojima, T. H. Painter,
 W. J. Parton, and A. R. Townsend. 1994. Climatic, edaphic, and biotic controls over storage and turnover of carbon in soils. Glob. Biogeochem. Cycles 8: 279–293.
- Schweizer, M., J. Fear, and G. Cadisch. 1999. Isotopic (13C) fractionation during plant residue decomposition and its implications for soil organic matter studies. Rapid Commun Mass Spectrom 7.
- Schwendenmann, L., E. Veldkamp, J. J. O'Brien, and J. Mackensen. 2003. Spatial and temporal variation in soil CO2 efflux in an old-growth neotropical rain forest, La Selva, Costa Rica. Biogeochemistry 64: 18.
- Scott-Denton, L. 2003. Spatial and temporal controls of soil respiration rate in a highelevation, subalpine forest. Soil Biol. Biochem. 35: 525–534.
- Shade, A., H. Peter, S. D. Allison, D. L. Baho, M. Berga, H. Bürgmann, D. H. Huber, S. Langenheder, J. T. Lennon, J. B. H. Martiny, K. L. Matulich, T. M. Schmidt, and J. Handelsman. 2012. Fundamentals of Microbial Community Resistance and Resilience. Front. Microbiol. 3. Available at: http://journal.frontiersin.org/article/10.3389/fmicb.2012.00417/abstract [Accessed]
 - March 23, 2021].
- Smith, J. E., A. D. Cowan, and S. A. Fitzgerald. 2016. Soil heating during the complete combustion of mega-logs and broadcast burning in central Oregon USA pumice soils. Int. J. Wildland Fire 25: 1202.
- Smith, N. R., B. E. Kishchuk, and W. W. Mohn. 2008. Effects of Wildfire and Harvest Disturbances on Forest Soil Bacterial Communities. Appl. Environ. Microbiol. 74: 216–224.
- Stevens-Rumann, C. S., K. B. Kemp, P. E. Higuera, B. J. Harvey, M. T. Rother, D. C. Donato, P. Morgan, and T. T. Veblen. 2018. Evidence for declining forest resilience to wildfires under climate change F. Lloret (Ed.). Ecol. Lett. 21: 243– 252.
- Stohlgren, T. J., and R. R. Bachand. 1997. Lodgepole Pine (Pinus contorta) Ecotones in Rocky Mountain National Park, Colorado, USA. Ecology 78: 632–641.
- Switzer, J. M., G. D. Hope, S. J. Grayston, and C. E. Prescott. 2012. Changes in soil chemical and biological properties after thinning and prescribed fire for ecosystem restoration in a Rocky Mountain Douglas-fir forest. For. Ecol. Manag. 275: 1–13.
- Thompson, I. D. 2009. Forest resilience, biodiversity, and climate change: a synthesis of the biodiversity / resiliende / stability relationship in forest ecosystems. Secretariat of the Convention on Biological Diversity, Montreal.
- Tieszen, L. L., and T. W. Boutton. 1989. Stable Carbon Isotopes in Terrestrial Ecosystem Research. *In* P. W. Rundel, J. R. Ehleringer, and K. A. Nagy (Eds.) Stable Isotopes in Ecological Research. Ecological Studies. pp. 167–195, Springer New York, New York, NY. Available at: http://link.springer.com/10.1007/978-1-4612-3498-2_11 [Accessed March 19, 2021].
- Turner, M. G., K. H. Braziunas, W. D. Hansen, and B. J. Harvey. 2019. Short-interval

severe fire erodes the resilience of subalpine lodgepole pine forests. Proc. Natl. Acad. Sci. 116: 11319–11328.

- U.S. Climate Change Science Program. 2007. The First State of the Carbon Cycle Report (SOCCR): The North American Carbon Budget and Implications for the Global Carbon Cycle. 264.
- USFS. 2013. FSH 1909.12 Land Management Planning Handbook.
- Walker, L. R., D. A. Wardle, R. D. Bardgett, and B. D. Clarkson. 2010. The use of chronosequences in studies of ecological succession and soil development: Chronosequences, succession and soil development. J. Ecol. 98: 725–736.
- Walker, X. J., J. L. Baltzer, S. G. Cumming, N. J. Day, C. Ebert, S. Goetz, J. F. Johnstone, S. Potter, B. M. Rogers, E. A. G. Schuur, M. R. Turetsky, and M. C. Mack. 2019. Increasing wildfires threaten historic carbon sink of boreal forest soils. Nature 572: 520–523.
- Whitlock, C., S. L. Shafer, and J. Marlon. 2003. The role of climate and vegetation change in shaping past and future fire regimes in the northwestern US and the implications for ecosystem management. For. Ecol. Manag. 178: 5–21.
- Wright, C. S., A. M. Evans, S. Grove, and K. A. Haubensak. 2019. Pile age and burn season influence fuelbed properties, combustion dynamics, fuel consumption, and charcoal formation when burning hand piles. For. Ecol. Manag. 439: 146– 158.
- Yang, Y., R. T. W. Siegwolf, and C. Körner. 2015. Species specific and environment induced variation of Î'13C and Î'15N in alpine plants. Front. Plant Sci. 6. Available at: http://journal.frontiersin.org/Article/10.3389/fpls.2015.00423/abstract [Accessed March 22, 2021].
- Yavitt, J. B., and T. J. Fahey. 1986. Litter Decay and Leaching from the Forest Floor in Pinus Contorta (Lodgepole Pine) Ecosystems. J. Ecol. 74: 525.
- Zhang, D., D. Hui, Y. Luo, and G. Zhou. 2008. Rates of litter decomposition in terrestrial ecosystems: global patterns and controlling factors. J. Plant Ecol. 1: 85–93.
- Zinke, P. J. 1962. The Pattern of Influence of Individual Forest Trees on Soil Properties. Ecology 43: 130–133.
- Zon, R., and R. N. Cunningham. 1931. Logging slash and forest protection. Wis. Res. Bull. 40.