EFFECTS OF WILDFIRE ON SOIL CARBON BIOAVAILABILITY IN FORESTED

ECOSYSTEMS OF COLORADO

A THESIS

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1. ABSTRACT

Given a trend of increasing wildfire frequency and intensity in the Western U.S., it is important to understand how the recovery and resilience of forest C stocks are impacted by severe fire. The purpose of this study was to look at how fire affected the size and relative bioavailability of soil C stocks, influencing rates of C mineralization. Study sites were in a montane Ponderosa Pine forest of Central Colorado and a subalpine Lodgepole Pine forest of Northern Colorado. I measured terrestrial C stocks and soil C bioavailability in plots burned in the 2002 Hayman and Hinman fires as well as undisturbed reference plots in each forest. Analyses included estimates of charcoal, aboveground biomass C, soil (top 10 cm) and water-extractable C and N. Soil incubation experiments were also conducted to measure the rate of microbial respiration per g soil C (a proxy for relative bioavailability). Total terrestrial C was ~53% lower in the montane ecosystem relative to the subalpine ecosystem, and >50% lower in burned plots relative to reference plots in both ecosystems. Soil C bioavailability did not vary with fire history in the subalpine forest, but was ~44% higher in burned plots in the montane forest. These results suggest that fire resulted in a significant reduction in terrestrial C storage. In addition, soil C bioavailability depended on plant regrowth. In the montane ecosystem, there were no tree seedlings in burned plots; as a result, C inputs to soil came primarily from grass and forb litter, which is more bioavailable than woody material. Comparatively rapid reestablishment of saplings in the subalpine forest meant that the quality of the soil C pool was similar in burned and undisturbed plots. Therefore, ecosystem response to wildfire differed with forest type, and lasting effects of wildfire on the quantity and bioavailability of soil C was determined by regrowth of trees.

2. INTRODUCTION

2.1 Background

Forest ecosystems represent a significant global carbon pool. Forests are estimated to cover approximately 4.1 billion hectares and contain 1240 Pg C (Lal 2005), acting as a net carbon sink (Dore et al 2008). Wildfire is a natural source of disturbance which plays an important role in regulating flows of matter and energy through forest ecosystems. Biomass burning releases between 2 & 6 Pg C globally each year (Knicker 2007). In general, carbon released to the atmosphere from the loss of aboveground vegetation and soil organic matter is re-sequestered during post-fire regrowth (Czimczik et al. 2003, González-Pérez et al. et al. 2004). However, severe disturbance can shift the net carbon balance of forests (Dore et al. 2008).

Looking at paleoecological records of past disturbance events, McLauchlan et al. (2014) show linear rates of C accumulation in aboveground live biomass following a disturbance event, which in turn leads to C accumulation in soil pools, eventually returning the system to prefire conditions. Thus, they conclude that if there are no fundamental shifts in the ecosystem composition or environmental factors, the net ecosystem carbon balance trends toward zero over the long term. However, a change in the disturbance regime (e.g. fire frequency and intensity) can lead to a fundamental shift in the ecosystem carbon balance, which in turn can impact the global carbon balance (McLauchlan et al. 2014).

Recent studies provide evidence of a climate-induced regime shift for wildfire in the western U.S. (Westerling et al. 2006, Moritz et al. 2012). Higher spring and summer temperatures and earlier snowmelt are linked with increased fire frequency and intensity

(Westerling et al. 2006). In addition, a history of fire suppression throughout the Western

U.S. has disrupted the natural fire regime of many forests, especially Ponderosa pine

(*Pinus ponderosa*) forests, changing stand density and fuel structure (Veblen et al. 2000).

The result is increased likelihood of stand-replacing crown fires. Colorado is a good

example of this trend, with a number of severe fires occurring in the past fifteen years,

including the Hayman fire of 2002, the Waldo Canyon, Fourmile and High Park fires of

2012, and the West Fork fire in 2013. . A fundamental shift in the fire regime may disrupt

the ability of terrestrial ecosystems to sequester carbon (Dore et al. 2008). Studying the

factors involved in recovery and resilience of forested ecosystems is therefore relevant to

understanding the feedbacks associated with disturbance and climate change.

Forests dominated by Ponderosa pine and Douglas fir (*Pseudotsuga menziesii*),

are characterized by frequent surface fires. Veblen et al. (2000) found an average

historical fire-return interval of 6-15 years in the Colorado Front Range. These low-

intensity fires determine community composition and structure. Adult Ponderosa pine

and Douglas fir are both fire-adapted. However, Ponderosa pine saplings as small as 5 cm

in diameter are able to withstand surface fires (Graham and Jain 2005), whereas fires tend

to kill young Douglas fir and understory vegetation (Veblen et al. 2000). This maintains

an open canopy and prevents fuel accumulation (Veblen et al. 2000). Regrowth after

surface fires is rapid, and some studies have shown that low-intensity fires generally have

a small effect on soil properties and nutrient loss (Hatten et al. 2005, Wuthrich et al.

2002). However, a history of fire exclusion in the Western U.S. has allowed Ponderosa

pine to be succeeded by shade-tolerant, late successional species (i.e. Douglas fir) in

some areas, leading to forests with denser fuel structures (Graham and Jain 2005). This

allows fire to spread to the canopy, resulting in catastrophic crown fires. Crown fires can be extremely destructive, destroying large areas of forest and affecting soil physical properties and C stocks (Graham and Jain 2005).

In contrast to montane Ponderosa pine ecosystems, the natural fire regime in subalpine mixed conifer forests dominated by Lodgepole pine (*Pinus contorta*) is characterized by infrequent severe fires (Lotan and Critchfield 1990). Lodgepole pine is adapted to reproduce via both serotinous and non-serotinous cones, allowing forests to regrow from fire-opened seeds after a stand-replacing fire (Lotan and Critchfield 1990). These forests, which are naturally denser than Ponderosa pine forest, are less impacted by fire suppression. Nevertheless, a climate change- induced disturbance regime shift could affect the productivity and long-term carbon balance of these forests.

With the drastic reduction in net primary production, forests often become sources of carbon for years to decades following a stand-replacing fire (e.g. Dore et al. 2008, 2012, Marañon-Jimenez et al. 2011, Law et al. 2003). Dore et al. (2008, 2012) found that ecosystem respiration exceeded photosynthesis for at least fifteen years following a stand-replacing fire in an Arizona Ponderosa pine forest. Similarly, Law et al. (2003) found that in a chronosequence of Ponderosa pine forest in Oregon, average NEP was -124 g C m^{-2} yr^{-1} in Ponderosa pine forests 9-24 years old. Total ecosystem carbon storage reached its maximum at 150-200 years of development, with average NEP of 170 g C m^{-2} yr^{-1} in mature stands (Law et al. 2003). For Lodgepole pine forest, regrowth has been estimated to recover the C deficit of a crown fire after 250 years (DeLuca and Aplet 2008). The time for total C storage to return to prefire levels after a stand-replacing fire is therefore on the scale of centuries. A shift in the disturbance regime due to climate

change has important implications for the long-term trajectory of carbon cycling in theses ecosystems (McLauchlan et al. 2014). If recovery of C stocks cannot keep pace with losses from increased fire frequency and intensity, forests in the Western U.S. could shift to a net source of C over the long term. Therefore, it is important to understand the mechanisms by which severe fire influences recovery and resilience of carbon stocks to understand how a change in disturbance regime could affect the regional C budget.

2.2 Effects of Fire on Ecosystem Processes

The direct and indirect effects of fire on ecosystems are highly dependent on fire intensity and duration, as well as preexisting ecosystem characteristics (Certini 2005). Fire affects ecosystems through biomass burning and subsequent changes in soil, hydrological processes, and nutrient availability (Marañon-Jimenez et al. 2011). Severe fire releases large quantities of carbon stored in vegetation, litter, and soil into the atmosphere as CO_2. Aboveground biomass that is not fully oxidized remains as dead standing trees ("snags"), coarse woody debris (CWD), particulate soil organic matter (SOM) and charcoal. High-intensity fire can cause a near total reduction in the litter and soil organic layers (e.g. Buma et al. 2014, Knicker 2007). Soil organic matter and biomass that is not fully oxidized undergoes heat-induced changes in structure and composition, which affects its biodegradability, and, subsequently, the ecosystem's C sequestration potential (González-Pérez et al. 2004, DeLuca and Aplet 2008). As soil is generally the largest terrestrial C stock (González-Pérez et al. et al. 2004), and soil conditions influence regrowth of vegetation, studying soil dynamics is relevant to the overall C balance.

2.2.1 Soil Nutrients

Fire results in significant short-term effects on soil nutrient availability by releasing carbon, nitrogen, and other nutrients stored in complex organic molecules. While soil tends to be a good insulator, in high-intensity fire it can reach extreme temperatures, up to 900 ^{O}C near the soil surface (Ice et al. 2004). In these cases, direct volatilization of soil nutrients such as N and P may occur (e.g. Ice et al. 2004, Murphy et al. 2006). N is particularly sensitive to volatilization, with a threshold temperature as low as 200 °C (Ice et al. 2004). In cases of low to moderate severity burn, partial combustion of litter and SOM can result in short-term increases in available soil nutrients (Covington et al. 1992). For instance, a number of studies have found higher concentrations of inorganic N in soil and higher rates of nitrification immediately following fire (Covington et al. 1992, Rhoades et al. 2011). This results in increased lateral exports of nitrate to streams (Schindler et al. 1980, Murphy et al. 2006, Smith et al. 2011, Rhoades et al. 2011). As a result, ecosystem N losses are a common effect of fire; this can have implications for the ecosystem nutrient balance, and thus affects both soil processes and regrowth (Rhoades 2011).

Interestingly, the fertilizing effect of nutrient-rich ash, along with changes in soil microclimate, often results in increased soil respiration in the short term (González-Pérez et al. 2004, O'Neill et al. 2006, Knicker 2007). Wuthrich et al. 2002 found elevated soil respiration for several months following fire in a sweet chestnut forest, with no increase in microbial biomass. This suggests that post-fire loss of ions is not likely to be mitigated by incorporation into microbial biomass (Wuthrich et al. 2002). Kranabetter et al. (2015)

posit that ecosystems are sensitive to increases in fire intensity or frequency if nutrient loss exceeds supply, affecting long-term ecosystem productivity.

2.2.2 Hydrology

Indirect effects of fire include changes to soil and hydrologic processes. For example, soils in burn scars often show fewer soil aggregates, increased bulk density and decreased water-holding capacity (WHC) due to the loss of soil organic matter (Certini 2005). Fire-induced changes to soil organic compounds also contribute to soil hydrophobicity, compounding the problem of decreased water holding capacity (González-Pérez et al. 2004, Knicker 2007, Certini 2005, Ice et al. 2004). This results in a decrease in infiltration rates, allowing overland flow to occur (Moody and Martin 2001). Further, the loss of plant cover reduces evapotranspiration, and interception from canopy and litter/duff is reduced, affecting hydrologic pathways. As a result, most studies show increased post-fire runoff and erosion (Moody and Martin 2001), leading to potentially substantial losses of C, N, and base cations through export of sediments and particulate organic matter (Murphy et al. 2006). Thus, increased nutrient exports through both leaching and accelerated erosional processes can result from loss of plant cover.

This has important implications for the ecosystem carbon balance; besides impacting water quality and stream health (Smith et al. 2011), changes to the hydrology of burned watersheds also influence biogeochemical cycles. Increased erosion and loss of SOM and nutrients, as well as decreased soil water availability, limits the rate of vegetative recovery, with important implications for the C balance (Knicker 2007). In addition, interactions between terrestrial and aquatic systems should be considered. Recent work illustrates that the lateral export of C from terrestrial ecosystems is not

negligible relative to terrestrial net ecosystem production (e.g. Aufdenkampe et al. 2011). Rather, rivers and streams process substantial quantities of C, which is returned to the atmosphere as CO_2, stored in sediments, or eventually delivered to the ocean (Aufdenkampe et al. 2011). Gaseous CO_2 losses from streams and rivers represent a significant C source on the global scale, accounting for an estimated 1.8 Pg C annually (Raymond et al. 2013). Thus, particulate and dissolved organic matter exported from terrestrial ecosystems could significantly affect gaseous CO_2 losses from aquatic ecosystems. Further, Olefeldt et al. (2013) found that UV-mediated degradation of dissolved organic matter in aquatic ecosystems can lead to rapid mineralization of aromatic compounds. Interestingly, even pyrogenic substances considered to be recalcitrant may have pathways for rapid degradation (Olefeldt et al. 2013). This suggests that, in considering the effect of fire on C cycling, it is important to consider the lateral flows from terrestrial ecosystems to inland waters.

2.2.3 Soil Respiration

Another indirect effect of fire important to understanding C cycling is its influence on rates of soil C mineralization rates. Initially, fire causes a decrease in microbial biomass, favoring bacteria over fungi (Knicker 2007). Studies have shown varying effects of fire on microbial biomass and respiration over time. Some show a rapid return of microbial biomass to pre-fire levels (e.g. Wuthrich et al. 2002), while others required years to recover microbial and fungal biomass (Knicker 2007). However, given that the majority of soil microbes are inactive at any given time, microbial activity tends not to be directly dependent on microbial biomass (Chapin 2011). Rather, microbial activity depends on substrate quantity and quality, as well as environmental and

community factors (Buchmann 2000). Soil substrate consists of microbial biomass, C inputs from vegetation and CWD, and the remnant soil organic pool, the size and composition of which is a function of fire intensity and duration (González-Pérez et al. 2004). Often, increased soil temperature, pH, and nutrient availability enhance mineralization of remaining SOM immediately following a fire (Certini 2005, Wuthrich et al. 2002, O'Neill et al. 2006). However, the loss of vegetation decreases C inputs, depressing microbial activity until vegetation regrows (Knicker 2007). Therefore, the soil C balance within the first decades following a fire depends on regrowth of vegetation, as well as the quantity and quality of organic matter that was not fully combusted. Importantly, soil C quality influences microbial respiration rates, which affects the ecosystem C balance during recovery.

Direct effects of fire on organic materials tend to decrease biodegradability (Olefeldt et al. 2013, González-Pérez et al. 2004). Fire produces char, or black carbon, a mixture of pyrogenic C-enriched aromatic compounds which are considered to be extremely recalcitrant (DeLuca and Aplet 2008). Heating causes a decrease in the atomic H/C ratio and O/C ratio, suggesting increased aromaticity and decreased solubility (González-Pérez et al. 2004). In addition to various important physical properties in soils, char is resistant to microbial degradation (DeLuca and Aplet 2008). Though there is significant disagreement as to how much of char produced by fires ends up stored in the passive soil C pool, estimates put mean residence times at 3000-12,000 years, with 50-270 Tg of black carbon produced annually (DeLuca and Aplet 2008, Knicker 2007). Others estimate the microbial degradation half-life of black carbon in the range of 500-1000 years (Poore 2014). Fire thus has the potential to sequester large quantities of

carbon in the stable soil C pool. However, Buma et al. (2014) found that in a Lodgepole

pine forest of Northern Colorado, the proportion of black carbon did not differ between

forest plots that have experienced recent high-intensity fire and undisturbed plots (though

it was higher in burned plots). This suggests that given a history of periodic fire events,

the quantity of recalcitrant carbon in soil is not significantly impacted by a specific fire

disturbance event, even a severe one (Buma et al. 2014). Other studies have also shown

that recent fire history affects surface and aboveground char, while mineral soil char is

less affected (DeLuca and Aplet 2008). Addition of newly formed char to the soil C pool

depends on soil mixing; some may be eroded, degraded, or combusted in subsequent fire

and therefore not stored in soils (DeLuca and Aplet 2008). Thus, it is difficult to quantify

the long-term effect of severe fire on the composition of the soil C pool.

2.3 Research Questions

If recovery of ecosystem C stocks and soil nutrients cannot keep pace with

increased fire frequency and intensity, it is possible that the ecosystem C balance will

shift (Kranabetter et al. 2015). This suggests a possible positive feedback with climate

change. Therefore, it is important to understand the mechanisms which determine the

recovery and resilience of soil C pools and the long-term implications for the ecosystem's

response to disturbance. While a number of studies have looked at the size of C stocks

and the factors involved in determining soil respiration rates (e.g. Dore et al. 2008, 2012,

Hatten et al. 20015, Buchmann 2000, O'Neill et al. 2006, Wuthrich et al. 2002, Law et al.

2003, Marañon-Jimenez 2011), it is still poorly understood how soil C bioavailability

varies with fire history. This study aims to improve our understanding of the dynamics of

C cycling in forest ecosystems over time after severe fire, focusing on substrate quantity and quality. I measured soil and aboveground C and N stocks and soil C quality via laboratory incubation experiments, and provided estimates of stream exports. Study sites were within the Hayman fire area (montane Ponderosa pine forest of the Colorado Front Range) and the Hinman fire area (subalpine Lodgepole pine forest of Northern Colorado) (Map 1) . Both crown fires occurred in 2002.

I hypothesize that soil C bioavailability is lower in the burned areas relative to the undisturbed forests. Since the fires occurred thirteen years prior to sampling, it is expected that any nutrient flush immediately following fire would have subsided. While O'Neil et al. (2006) found increased decomposition of humic materials in burned Black spruce forest for seven years after fire, most studies show elevated rates of soil respiration in the first year or two (Wuthrich et al. 2002, Knicker 2007, González-Pérez et al. 2004). Over time, with low NPP, there is likely to be a reduction in soil C and nutrient pools, resulting in depressed overall microbial activity relative to unburned sites (Dore et al. 2008). In addition, measures of soil C bioavailability may provide evidence for a pool of recalcitrant pyrogenic compounds produced from the incomplete combustion of plant and soil organic material. An increase in the size of the passive soil C fraction might help to buffer the effect of fire shifting the ecosystem to a net C source, impacting the long-term C balance.

By focusing on C stocks and soil C bioavailability, I attempt to tease out the mechanisms involved in C cycling thirteen years after severe fire in these ecosystems, including interactions between vegetation, soils, and hydrology. My research will address the following questions:

1) How does the bioavailability of carbon in soils compare between disturbed and undisturbed ecosystems (burned vs. control watersheds)?

2) How does the bioavailability of carbon in soils compare between montane *P. Ponderosa* forest and subalpine *P. Contorta* forest? How does ecosystem type affect the response of soil C pools to fire (Hayman vs. Hinman burns)?

3) What are the implications of soil carbon bioavailability for post-fire recovery and resilience of forested ecosystem carbon stocks?

3. METHODS

3.1 Study Area

3.1.1 Central Colorado

The study area included eight forested watersheds in the Colorado Front Range. Three were unburned, two were affected by the 2012 Waldo Canyon Fire, and three were affected by the 2002 Hayman fire (Table 1). Stream sampling began in June 2015 and continued weekly through August 2015. In addition to stream sampling, terrestrial plots were established in four of the watersheds which had accessible terrain. Three 15x15 m plots were established in each watershed at different hillslope positions (crest, mid-slope, and toe slope). Soil samples were collected in June 2015 and a carbon census was conducted in each plot. GIS analysis quantified burn severity and extent in each watershed (Table 1).

The Hayman Fire began on 8 June 2002 and was not declared extinguished until 30 October 2002. Affecting 558 km^2 (Map 2B), it was the largest fire in recent Colorado

History (Rhoades 2011). The fire burned in lower montane forests (elevation 1980-2750m), dominated by Ponderosa pine and Douglas fir (Figure 1). Mean annual temperature is 9.4^{o}C and mean annual precipitation is ~60 cm (Stevens, 2012), 19% of which comes from snowfall (wunderground.com). However, the period of sampling occurred during unusually high summer precipitation (~15 cm in June & July 2015) (PRISM climate data). Two watersheds affected by the Hayman Fire, near Deckers, CO, were included in the soils study. However, analysis in GIS showed that the Fourmile Creek watershed was also affected in part of its area by the adjacent 2002 Schoonover fire, and our plots fell within the Schoonover fire area rather than the Hayman area. As the fires occurred within the same month, I will refer to the plots within the Schoonover fire as belonging to the Hayman fire area, for simplicity. One nearby unburned watershed with similar characteristics was also included as a reference (Map 1). In the burned areas, there was no live tree cover, but there were grasses, forbs and succulents (Fig. 2). Soil collection and terrestrial analysis occurred June 4-9, 2015, just before the peak of the growing season. The area is underlain by the Pikes Peak batholith, course-grained biotite granite (Stevens 2012). Soils are well-drained sandy loams, classified as Typic Ustorthents and Typic Cryorthents (Stevens 2012).

The Waldo Canyon Fire was ignited 23 June 2012 and burned across 74 km^2 northwest of Colorado Springs, CO (The Denver Post). It was fully contained on 10 July 2012. While not as extensive as the Hayman fire, it had greater human impacts, destroying a number of homes. The area has similar climate, soil, and ecosystem characteristics to the Hayman fire area, and therefore lends itself well to a comparison of carbon stock recovery over time. However, there is significantly greater forest cover in

the Waldo Canyon study area as compared with the Hayman study area, though the fire was more recent. The area is dominated by Ponderosa pine, with an understory of Gambel oak (*Quercus gambelii*), Mountain mahogany (*Cercocarpus montanus*), grasses and forbs. The Dry Creek watershed, classified as low severity burn, was included in the soils study. However, the watershed was steep enough that there was no toe slope accumulation zone, so only two terrestrial plots were analyzed (crest and midslope). An unburned watershed in the Waldo Canyon area was not included because of limited access; as a result, the comparison between the Dry Creek plots and the Hayman burn plots is mostly anecdotal.

3.1.2 Northern Colorado

The study also included twelve terrestrial plots in the Routt National Forest north of Steamboat Springs, CO, which were not grouped by watershed, but were documented in Buma et al. (2014) (Map 2A). Soils from twelve of the plots were resampled to compare the effects of ecosystem type on soil carbon stock recovery. Six of the plots were burned, affected by the severe 2002 Hinman fire, and six were undisturbed. The Hinman fire burned 144 km^2 in the Routt National Forest, starting August 2002. Since the Hinman fire occurred in the same year as the Hayman fire, a comparison of soil C quantity and quality in both areas shows how ecosystem type influences recovery and resilience of C pools.

The study plots were within subalpine forests ranging from 2,500 to 3,300 m in elevation (Buma et al. 2014) (Fig. 2). The ecosystem is dominated by Lodgepole pine, as well as a mix of Engelmann spruce (*Picea engelmannii*), Subalpine fir (*Abies lasiocarpa*), and Aspen (*Populus tremuloides*) (Buma et al. 2014). Mean annual

precipitation is approximately 110.2 cm (National Water and Climate Center), >30% of which falls as snow during winter months (wunderground.com). Soils are Cryochrepts and Dystrocryepts from glacial deposits, granite and gneiss (Buma et al. 2014) with a thin organic layer overlying sandy loam soils (Stevens 2012).

3.2 Carbon Census

The Front Range watersheds were selected using GIS analysis; Map 1 shows plot locations. They were selected to have similar ecosystem characteristics (dominant vegetation, bedrock, climate), and represent a range of fire histories. Terrestrial carbon census and soil sampling was conducted in four of the nine watersheds, selected based on accessibility. Fifteen by fifteen meter terrestrial plots (three in each watershed) were chosen to represent different hillslope positions (Fig. 3). The Dry Creek watershed was steep, with no toe slope accumulation zone outside of the riparian area. In the Dry Creek, Pine Creek, and Painted Rocks sites, there was abundant riparian vegetation, largely dominated by willow (*Salix depressa* and *Salix monticola*) (Powell 2013). In the Fourmile Creek watershed, the valley narrowed toward the bottom, limiting the size of the toe slope plot to 15 by 7.5 meters. Exact plot locations were recorded for further analysis in GIS, using a Trimble GPS unit (Map 2). Carbon pools in each plot were estimated using methods from Buma et al. (2014), including understory, course woody debris (CWD), live trees, dead standing trees ("snags"), and soil carbon (top 10 cm).

The plots within the Routt National Forest were located using GPS coordinates from Buma et al. (2014) and identifying flags left from the previous study delineating plot boundaries. Total carbon was calculated for the Routt National Forest plots in the

paper by Dr. Buma, and therefore not repeated in this study. Soil sampling was repeated, however, and soil C stocks re-measured for the Routt National Forest plots.

3.2.1 Ground cover

In each Front Range plot, percent ground cover of graminoids, forbs, woody plants, moss/lichen, succulents, litter/duff, woody debris, rock, and dirt/gravel was estimated for 40 randomly located 0.25 m^2 quadrats. To measure biomass, 0.25 m^2 samples of graminoids (n=2), forbs (n=1), and pine litter (n=1) were collected. All vegetation in each square was clipped, dried in an oven at 55-60°C for 24 hours (or until fully dry), and weighed to determine the dry density (g m^{-2}). Subsamples of forbs, graminoids, and litter were dried and ground for elemental analysis of %C and %N. In addition, samples of branches and leaves from Gambel oak and Mountain mahogany were collected and analyzed for %C and %N, to determine the C content of shrubs. The carbon pool of litter, graminoids, forbs, and woody shrubs was calculated by multiplying biomass density by percent cover by percent carbon, and summed to get the total g C per plot in understory vegetation (excluding tree saplings) and litter. Moss and succulents were generally very small percentages, and considered negligible for total carbon. C content of coarse woody debris was calculated separately.

3.2.2 Course Woody Debris

Two 15 m Brown's transects were conducted for each Front Range plot to estimate CWD, following Brown's (1974) method. Transects were perpendicular to each other, crossing in their centers, one parallel to the slope and one perpendicular to the slope. The slope of each transect was measured using a clinometer. Fuel height and duff depth were measured at 1m and 3m for each transect. All 1-hour fuel (0-0.25 inches

diameter) intersecting transects in the first 2 m were counted, and the number charred

was recorded. The same was done for 10-hour fuel (0.25-1 inches diameter) in the first 5

m of transects, and 100 hour fuel (1-3 inches diameter) in the first 10 m. The diameter

was measured for all 1000 hour fuel (>3 inches diameter) intersecting the Brown's lines

along the full length, and the degree of decay was estimated. In addition, the proportion

of the circumference with char and the depth of char on each of the downed logs were

recorded. This data was used to calculate the total C stock of coarse woody debris

(calculations done by Dr. Buma, University of Alaska). Black carbon from CWD was

also calculated by calculating the volume of char around the circumference of charred

woody debris, and converting to Mg BC ha^{-1} by assuming 405 kg m^{-2} initial wood

density, 70% mass lost upon burning, and 75% C in remaining mass (Buma et al. 2014).

3.2.3 Trees

All living trees in each plot were counted and identified; several burned plots in

the Hayman burn area had no live trees. Seedlings (<1.5m) were measured for height. For

trees taller than 1.5m, diameter at breast height (DBH) was measured and height was

calculated by measuring distance from trunk, angle to base, and angle to top using a

clinometer. Biomass was calculated by Dr. Buma (University of Alaska) using allometric

equations from Jenkins et al. (2003). Total carbon calculations for living trees assumed a

carbon content of 50%.

Total carbon and BC of dead standing trees ("snags") were also estimated using

methods from Buma et al. (2014). Height and DBH of all dead standing trees were

measured. Volume was calculated using species-specific tapering equations from Kozak

et al. (1969) and adjusting DBH for the absence of bark. For broken snags, volume was

determined by projecting an unbroken height. Carbon was calculated assuming 405 kg m$^-$^{3} wood and 50% C by mass (Buma et al. 2014). To determine BC of snags, the proportion of circumference with char, height and depth of char was estimated. This was used to calculate the char volume, which was converted to Mg BC ha^{-1} by assuming 405 kg m^{-2} initial wood density, 70% mass lost upon burning, and 75% C in remaining mass (Buma et al. 2014). Calculations were done by Dr. Buma (University of Alaska).

3.3 Soil

In each plot, soil cores (top 10 cm) were collected at random locations using a 7 cm diameter bulb planter. For soils with distinct mineral and organic horizons, mineral and organic soils were separated and the depth of the organic layer was recorded. In most burn areas, there was only mineral soil. Ten samples were collected in each of the Front Range plots, and five were collected in each of the Routt National Forest plots. For three samples from each plot, the full core was kept. For each of the remaining soil samples, the sample was mixed in the field, and a subsample of approximately half the corer volume was brought back to the lab for analysis.

Soils were kept cool in sealed bags until they could be processed. Two full core soil samples from each plot were weighed, oven dried, and weighed again. Percent moisture was calculated as the mass difference between wet and dry weights, divided by the wet weight. Bulk density was calculated by dividing the dry weight by the volume of the corer. All soil samples were sieved through a 2 mm filter to divide them into fine and course fraction. For 3 soil samples per plot, a portion of undried or "wet" fine fraction soil was used for the incubation experiment (described below). "Wet" fine fraction soil

was also used for soil extractions (described below). Fine fraction density (g mL^{-1}) was calculated by weighing a known volume of "wet" fine fraction soil, using a 10 mL graduated cylinder. A portion of fine fraction soil from each soil sample was dried in an oven at ~55°C for 24 hours and ground into powder using a Certiprep 8000 Mixer/Mill soil grinder. Powdered soils (n=3 per plot, the same samples that were used for incubations) were analyzed using an elemental analyzer for %C and %N, which was used to calculate total C of fine fraction soil. With each set of samples, six standards (0.5, 1, 2, 3, 6, and 8 mg) of atropine (4.84 % N, 70.56% C) were analyzed to generate a calibration curve. Samples of 15-20 mg of soil (5-10 mg for vegetation samples) were analyzed. Precision is ± 0.089 %N and ± 0.181 %C.

Course fraction soil was sorted by hand into roots/organic material, rocks, and charcoal, and weighed for each full core soil sample (n=2 per plot). This gave the total mass of course fraction soil for the area of the soil corer (7 cm diameter), and was used to calculate the mass of fine fraction soil per unit area. Course fraction soil C was calculated assuming 50% C by mass for roots and 70% C by mass for charcoal. Total soil C (top 10 cm) was determined as the sum of course and fine fraction soil C.

3.3.1 Soil Extractions

A subsample of "wet" fine fraction soil (~10 g) was combined with MilliQ water (~300 mL) in a beaker and agitated on a shaker table for 24 hours. The sediment-water slurry was filtered through a pre- combusted 0.7 μm glass microfiber filter (Whatmann GF/F). The extracted liquid was analyzed for dissolved organic carbon (DOC), total dissolved nitrogen (TDN), and dissolved ions. Extractable C and N are considered to be more readily available for leaching or uptake than total C and N.

DOC and TDN were measured on a Shimadzu TOC-L/ TNM-L unit. Standards (in the form of KHP and KNO_3, dissolved in MilliQ water) were run with each set of samples were run in duplicate for QA/QC. Samples with a high concentration of DOC and TDN (those with >1 specific UV absorbance at 254 nm, measured using an Agilent 8453 UV-vis spectrometer) were gravimetrically diluted with MilliQ water and run a second time to ensure that they wouldn't fall outside the calibration curve. Each sample underwent up to 5 injections, and mean peak area was calculated from the three most precise injections. Actual DOC and TDN concentrations in mg L^{-1} were calculated based on the standard curve, with precision of $\pm$ 0.688 mg L^{-1} DOC and $\pm$ 0.131 mg L^{-1} TDN. Precision was calculated as the average standard deviation between replicate measurements. All dilutions were done gravimetrically (significant to the thousandth of a gram).

Dissolved ions were measured for each soil extraction using a Dionex ICS-5000 ion chromatographer. Analyzed ions include: F^-, Cl^-, NO_2^-, SO_4^{2-}, Br^-, NO_3^-, PO_4^{2-}, Li^+, Na^+, NH_4^+, K^+, Mg^{2+}, Ca^{2+} (precision and range of each ion provided in Appendix I). A blank of MilliQ water and a replicate sample were run between every set of 15 samples. All dilutions were done gravimetrically.

3.3.2 Incubation Experiment

For three soil samples from each plot, a subsample of "wet" fine fraction (<2 mm) soil was incubated to measure aerobic soil respiration. 30-50 g of soil was placed in clear glass jars (353- 472 mL volume) and left uncovered in a controlled environment (5 °C, dark). Each week for seven weeks, soils were rewetted with MilliQ water to return them to their original moisture content, and covered with an airtight seal for two to three hours

to allow CO_2 to accumulate in the headspace of the jar. At the end of the accumulation period, 5 mL of air was extracted from the headspace of each jar using a gastight syringe and analyzed on a SRI-8610C gas chromatograph. To determine the baseline CO_2 concentration, ambient air (at least three samples) was analyzed. This assumed that the air was well-mixed, and therefore the initial CO_2 concentration in each jar would not differ significantly from the ambient air in the lab. The rate of soil respiration was calculated as the difference between the initial and final CO_2 concentrations divided by the time the jar was covered. A calibration curve was made from measurements of standard gases 101 and 1010 ppm CO_2. Two sets of standards were run with each set of samples, when possible; replacement standards were back-ordered for several weeks, and so an "averaged" calibration curve was used for those days. The instrument was shown to be quite robust; the coefficient of conversion between peak area and ppm did not differ by more than 0.15 over the study period, accounting for <6% of the variation in CO_2 ppm.

Respiration rates were measured weekly starting within 1 week of soil collection. Weekly measurements continued for seven weeks, and then respiration was measured again at 11 weeks to get a sense for the longer-term trend. The soil respiration rate was normalized to the C content of the soils to get mg CO_2-C per mg soil C per day, which was used as a proxy for relative soil carbon bioavailability. Soil respiration rates were used to extrapolate the total g C released per gram of soil carbon over the study period, which facilitated comparison between different fire histories and hillslope positions.

3.4 Stream Sampling

Weekly stream samples were collected through June and July 2015 and field stream measurements taken at each site, including discharge. Streams were sampled at the same location each time, and exact coordinates were recorded using a GPS unit (Map 2). To calculate discharge, total stream width was measured, and depth and velocity were recorded at several intervals (1 to 6 depending on stream size). Water samples were kept cool and brought back to the lab for further analysis. Samples were immediately filtered through a combusted 0.7 μm glass microfiber filter (Whatman GF/F) and stored in a refrigerator at 5 °C. Alkalinity was measured by titrating ~60 mL of unfiltered water using bromocresol green indicator and 0.012 M HCl (n=3 titrations for each stream each week). Carbonate concentration (i.e. dissolved inorganic C) was calculated from alkalinity measurements (assuming CO_3^{2-} is the major determinant of the buffering capacity). Stream samples were also measured for specific UV absorbance at 254 nm, which allowed SUVA for each sample to be calculated. SUVA is an indicator for the relative degree of aromaticity of dissolved organic compounds (Weishaar et al. 2003). UV absorbance was measured using an Agilent 8453 UV-vis spectrometer in a 1cm quartz cell. Samples with >1 absorbance at 254 nm were diluted with MilliQ water and rerun. Stream samples were also analyzed for DOC and TDN, using the same method for soil extractions.

For each watershed included in the stream analysis, fraction of area burned and burn severity were calculated in GIS using data from the national Monitoring Trends in Burn Severity dataset (MTBS.gov). Dividing discharge by watershed area provides water yield (m yr^{-1}). In addition, monthly precipitation for each watershed was obtained from PRISM climate data, and used to calculate the fraction of precipitation exported to

streams during the sampling period. This was used to compare how precipitation was partitioned in burned and unburned watersheds. Further, watershed area and measurements of discharge, DOC concentration, TDN concentration, and alkalinity were used to estimate C and N yield (g m^{-2} yr^{-1}) exported from each watershed, assuming that extrapolating from measurements taken during June and July accurately reflects nutrient export for the full year.

3.5 Statistics

Minitab 17 was used for all statistical analyses. Comparisons between groups (i.e. fire history, ecosystem type) were conducted using t-tests and Mann-Whitney tests. For normally distributed data sets, two-sample t-tests were used to test statistical significance for differences between the means of groups (i.e. fire history, ecosystem type). For data that was not normally distributed, nonparametric tests were used to determine significant differences between the medians of groups. Significance was defined as $p<0.05$, although given the small sample size, results with $p<0.1$ were reported on as well. Pearson's correlations and p-values were calculated to test significant correlations between variables, focusing on finding predictors for soil respiration, soil C bioavailability, and soil C:N. The normality of residuals for important relationships between variables was tested by graphing simple linear regressions and residual plots, using log transformations where necessary. Stepwise linear fit models were used to find significant predictors ($p<0.10$) for soil C bioavailability and control for multicollinearity between predictors (VIF close to 1). Linear fit models also allowed categorical differences between groups (i.e. ecosystem type) to be controlled for.

4. RESULTS

4.1 Total Carbon

Total carbon was estimated for each plot, and compared across ecosystem type

and fire history: Hayman Burn (n=6), Hayman Reference (n=3), Waldo Burn (n=2),

Routt/ Hinman Burn (n=6), Routt Reference (n=6). All estimates of terrestrial C stocks

(excluding soil data) for the plots within the Routt National Forest came from data

collected by Dr. Buma in 2011 using the same methods. Total carbon was higher in the

reference plots (114 Mg C ha^{-1}) relative to the burned plots (~54 Mg C ha^{-1}) in the

montane ecosystem, but the difference was not significant (Table 2). There was

moderately more total C in the subalpine undisturbed plots compared with the montane

($p<0.10$) (Fig. 4). Among the plots within the Routt National Forest, there was

significantly more total C in the unburned (240 Mg C ha^{-1}) compared with the burned

sites (99 Mg C ha^{-1}) ($p<0.05$). Aboveground biomass ranged from 0 Mg ha^{-1} in the Pine

Creek watershed in the Hayman fire area to 247 Mg ha^{-1} in the unburned plots within the

Routt National Forest (Fig. 4). It was consistently higher in unburned plots in both

ecosystems, but it did not differ significantly between the subalpine and montane

ecosystems. Coarse woody debris was significantly higher in the Hayman burn plots

(19.3 Mg C ha^{-1}) relative to reference plots (4.4 Mg C ha^{-1}), and significantly higher in

the subalpine (33.5 Mg C ha^{-1}) than the montane plots ($p<0.05$). It did not vary with fire

history within the subalpine plots.

Graminoids contained 43.5% C, with a density of 331.5 g m^{-2} dry weight (Table

3). Forbs contained 45.8% C with a density of 458 g m^{-2}. Total carbon of grass, forbs, and

shrubs did not differ significantly across sites. However, the percent ground cover of

litter was significantly higher in the reference plots (70.3 ± 25.2 %) relative to burned plots (27.9 ± 18.7 %) within the Hayman fire area. Percent cover of dirt and rocks was significantly lower in the Hayman reference plots (13.5 ± 11.2 %) relative to the burned plots (58.5 ± 23.3 %) (p<0.05). The same comparison was not made for the Routt plots, lacking data for % ground cover. As there was no char on snags or CWD in any of the unburned sites, the total non-soil black carbon was consistently higher in burned than control plots in both the Hayman and Routt areas.

4.2 Soil

Values for plot-level soil variables (e.g. bulk density, % moisture, total soil C) were determined by averaging measurements from two soil samples for each plot. Because bulk density measurements required drying a full core soil sample, the same soils used for these measurements could not also be used for incubations and extractions; therefore, these measurements were averaged for each plot. All soil measurements from both the Routt and Hayman sites came from soil samples collected in June and July 2015. Compared with control plots, bulk density (g cm^{-3}) was higher in burned plots in both the Hayman (p<0.1) and Routt (p<0.05) areas (Table 2). The undisturbed montane soils had significantly higher bulk density than subalpine soils (p<0.05). Conversely, soil moisture was moderately lower in the burned plots (5.7 ± 1.7 %) compared with control plots (9.4 ± 1.8 %) in the Hayman fire area (p<0.1) (Table 2). Soil moisture was significantly lower in the undisturbed Hayman plots than the undisturbed subalpine soils (p<0.05). Soil moisture did not differ significantly between burned (23.5 ± 5.89 %) and unburned soils (22.2 ± 8.5%) within the Routt National Forest.

Total soil C, including coarse fraction C and fine fraction C, did not differ

significantly between burned (15.1 ± 9.7 Mg C ha^{-1}) and control sites (16.3 ±8.8 Mg C

ha^{-1}) in the Hayman fire area (Fig. 4). Within the Routt National Forest, total soil C was

significantly lower in the disturbed plots (31.7 ± 14.4 Mg C ha^{-1}) relative to reference

plots (53.7 ± 11.6 Mg C ha^{-1}) ($p<0.05$). Soil C was also significantly greater in the

subalpine plots than the montane plots ($p<0.05$). Percent woody material of coarse

fraction soil was higher in control than disturbed sites in both the Hayman ($p<0.10$) and

Routt ($p<0.05$) areas, ranging from ~0.3% in the montane fire sites to >40% in the

subalpine undisturbed soils. It was significantly higher in the subalpine than montane

ecosystem ($p<0.05$). Percent charcoal of coarse fraction soil was also significantly higher

in the subalpine than montane ecosystem ($p<0.05$). Percent char ranged from ~0.07% in

the Hayman fire sites to ~3.2% in the subalpine undisturbed soils, though it did not vary

with fire history. Total soil carbon, as well as % char, % wood, and % moisture were

consistently higher in the Waldo Canyon fire plots relative to the Hayman burn plots

(Table 2), but given that n=2 plots in the Waldo Canyon watershed, there were no

statistically significant differences.

Measurements of %C & %N of fine fraction soil and extractable C, N, and ions

were estimated for three soils per plot. These were divided into groups to compare across

fire history and ecosystem type: Hayman burn (n=18), Hayman reference (n=14), Routt

Hinman burn (n=19), Routt reference (n=18), and Waldo Canyon burn (n=6). Soil carbon

and nitrogen in the montane sites was generally low, averaging 2.2 ± 1.7 % C and 0.10 ±

0.07 % N in the burned plots and 4.4 ± 3.5 % C and 0.18 ± 0.15 % N in the reference

plots. Burned soils in the subalpine plots averaged 4.9 ± 3.6 %C and 0.18 ± 0.14 %N,

while subalpine reference soils averaged 11.0 ±7.6 %C and 0.42 ± 0.27 % N (Table 2). The differences in soil C & N between the subalpine and montane ecosystems were significant (p<0.05). In both ecosystems, percent C and N of fine fraction soil was significantly higher in undisturbed plots relative to burned plots (p<0.05). In addition, %C and %N in the Waldo Canyon watershed (~ 2.8 and 0.14, respectively) exceeded that of Hayman burn soils. C:N of fine fraction soil was significantly lower in Hayman burned soils (25.8 ± 4.4) relative to reference soils (28.6 ± 3.6) (p<0.05), but did not differ significantly between burned (30.9 ± 8.8) and reference soils (30.4 ± 4.2) in the Routt Hinman area, or between ecosystems (Fig. 5).

4.2.1 Soil Extractions

Dissolved organic carbon (DOC) and total dissolved nitrogen (TDN) of soil extracts averaged 2.9 ± 1.7 mg C L^{-1} and 0.8 ± 0.36 mg N L^{-1}, respectively, in burned soils in the Hayman fire area. Hayman reference soils averaged 7.8 ± 3.7 mg C L^{-1} and 1.1 ± 0.6 mg N L^{-1}. The differences in DOC and TDN between burned and unburned soils in the Hayman area were significant (p<0.05). Within the Routt National Forest, burned soils averaged 5.9 ± 2.0 mg C L^{-1} and 1.0 ± 0.5 mg N L^{-1}, while unburned soils averaged 21.7 ± 16.4 mg C L^{-1} and 1.3 ± 0.7 mg N L^{-1}. Subalpine soil extracts had significantly higher concentrations of DOC and TDN relative to montane soils (p<0.05). DOC varied with fire history in the subalpine Routt soils (p<0.05), but there were no significant differences in TDN in the subalpine plots. The ratio of extracted C to N was significantly higher for unburned soils (8.9 ± 3.5) than burned soils (4.4 ± 1.9) in the montane Hayman area, and significantly higher for unburned subalpine soils (19.0 ± 5.4) relative to burned soils (7.9 ± 4.0) in the Routt National Forest (p<0.05) (Fig. 5). Extract

C:N was also higher in subalpine soils compared with montane soils, and higher in the Waldo Canyon burned plots (6.1 ± 1.4) than Hayman burn plots ($p < 0.05$) (Fig. 5).

Many of the ions measured in soil extracts were in such low concentrations that they fell below the detection limit. As a result, there were few significant differences in ion concentrations from fire history or ecosystem type (see Appendix I). However, a few differences are worth noting. Extracted calcium did not vary with fire history in the montane Hayman area, but it was higher in subalpine unburned soils (2.69 ± 2.65 mg L^{-1}) than subalpine burned soils (0.58 ± 0.82 mg L^{-1}) ($p < 0.01$). In the Hayman area, nitrate averaged 0.66 ± 0.41 mg L^{-1} in extracts from burn soils and 0.99 ± 0.83 mg L^{-1} from unburned soils, but the difference was not significant. In the Routt Hinman area, nitrate averaged 0.45 ± 0.49 mg L^{-1} from burned soils and 0.30 ± 0.41 mg L^{-1} from unburned soils, but again, due to large variability the difference was not statistically significant. Nitrate concentrations from the montane soils were moderately higher than subalpine soils, however ($p < 0.1$). Concentrations of extracted ammonium and nitrite were small relative to nitrate, accounting for, on average, ~25% of total inorganic N. As a result, inorganic N followed the same pattern as extract nitrate concentrations. Organic N averaged 0.31 ± 0.43 mg L^{-1} from unburned soils and 0.20 ± 0.38 from burned soils in the montane Hayman area; the difference was not statistically significant (Fig. 6). In the subalpine Routt forest, there were higher concentrations of extracted organic N from reference soils (0.99 ± 0.63 mg L^{-1}) relative to burned soils (0.63 ± 0.72 mg L^{-1}) ($p < 0.1$) (Fig. 6). Extracted organic N was significantly higher from subalpine soils than montane soils ($p < 0.01$).

4.2.2 Microbial Respiration

Respiration of incubated soils was measured over time and normalized to soil carbon as a proxy for relative soil C bioavailability (mg C-CO$_2$ g^{-1} C day^{-1}). Figure 7 shows normalized soil respiration rates over 7 weeks (with one additional measurement at 11 weeks), averaged for each of the Front Range watersheds and for burn and control plots within the Routt National Forest. While each set of soils shows high variability, there is a common pattern among the Front Range soils of an initial increase within the first 3-4 weeks, followed by a plateau of relatively consistent respiration rates (Fig. 7). Respiration from Routt soils stayed relatively constant throughout the study period.

In order to compare across fire history and ecosystem type, weekly respiration rates for each soil were summed over the seven-week study period. Total respiration of incubated soils (mg C-CO$_2$) was significantly higher for Routt control than Routt burn soils, and significantly lower for montane than subalpine soils ($p < 0.05$) (Fig. 8). While there were no significant differences in microbial respiration between burned and unburned soils from the Hayman Fire area, total respiration was significantly higher in the Waldo Canyon burn area than the Hayman burn ($p < 0.05$).

Soil C bioavailability of burned soils exceeded that of unburned soils in the Hayman area ($p < 0.05$, Figure 8B). Bioavailability was significantly higher for montane than subalpine soils ($p < 0.05$, Figure 8B), and moderately higher in the Waldo Canyon than the Hayman fire area ($p < 0.15$, Figure 8B). There were no significant differences in relative soil C bioavailability between burned and control plots in the Routt National Forest; however, there was higher variability in burned soils.

Soil C bioavailability was related not only to ecosystem type and fire history, but also to C and N stocks. For variables with values for each incubated soil sample (soil

respiration, %C, %N, DOC, TDN, ions), regressions were done with per sample data. For plot-level data (bulk density, soil moisture, C stocks), bioavailability measurements were averaged for each plot (n=3), reducing the total sample size for each variable. Appendix II has a full table of Pearson's correlations. Significant predictors (p<0.05) of soil C bioavailability included: %C of fine fraction soil (r= –0.546), %N (r= –0.532), C:N (r= –0.400), C:N of extract (r= –0.439), extract organic N mg L^{-1} (r= –0.294) bulk density (r= 0.583), soil % moisture (r= –0.429), total soil C Mg C ha^{-1} (r= –0.609), aboveground biomass Mg C ha^{-1} (r= –0.569), grass Mg C ha^{-1} (r= –0418), BC on CWD (r= 0.726), and % bare ground (r= 0.732). Moderate predictors (p<0.10) included: extract nitrate mg L^{-1} (r= 0.199) and calcium mg L^{-1} (r= 0.200). Figures 9 and 10 give several examples of linear regressions with soil C bioavailability. Soil C bioavailability was negatively correlated with soil carbon, C:N ratios, vegetation and soil moisture. Bulk density, black carbon, and bare ground cover were positively related with soil C bioavailability. Analysis with fit regression models showed that the best predictors for bioavailability (p<0.05, VIF<1.4) were total soil C (Mg C ha^{-1}), BC on CWD (Mg C ha^{-1}), extract TDN (mg L^{-1}), and extract Ca^{+} (mg L^{-1}). The model had R^2= 78.3%. However, controlling for fire history and ecosystem type showed that a number of these relationships, including the correlation with total soil C, were largely driven by the differences between the two ecosystems rather than by differences resulting from burn history.

4.3 Watershed Hydrology and Stream Chemistry

The hydrology of the Front Range watersheds also varied with fire history (Table 4). The fraction of precipitation (from PRISM data) exported as stream discharge was

significantly higher in the three burned watersheds in the Hayman area (0.83 ± 0.17) relative to the fraction of precipitation exported for the unburned Hayman watershed (0.021 ± 0.004) ($p<0.01$) (Fig. 11). The Waldo Canyon burned watersheds also had greater water export (0.62 ± 0.53) relative to the unburned watersheds (0.26 ± 0.21) ($p<0.01$). Water yield, calculated by normalizing discharge to watershed area, was also lower in the unburned watersheds relative to the burned watersheds in the Colorado Front Range ($p<0.10$). Water yield was 258.6 ± 94.8 m^3 ha^{-1} yr^{-1} in the Hayman reference watershed, 4505 ± 3756 m^3 ha^{-1} yr^{-1} in the Hayman burned watersheds, 6054 ± 6834 m^3 ha^{-1} yr^{-1} in the Waldo Canyon burned watersheds, and 2310 ± 1773 m^3 ha^{-1} yr^{-1} in the Waldo Canyon reference watersheds. Fraction exported was positively correlated with watershed slope ($r= 0.46$, $p<0.01$), and with fraction low severity burn ($r= 0.30$, $p<0.01$).

Total dissolved stream carbon (DIC + DOC) and nitrogen yield were estimated at 14 kg C ha^{-1} yr^{-1} and 4.1 kg N ha^{-1} yr^{-1} in burned watersheds in the Hayman area, and 1.9 kg C ha^{-1} yr^{-1} and 0.035 kg N ha^{-1} yr^{-1} in the Hayman reference watershed; these differences were significant ($p<0.001$). In the Waldo Canyon watersheds, reference streams averaged 11 kg C ha^{-1} yr^{-1} and 1.2 and kg N ha^{-1} yr^{-1} while burned streams averaged 15 kg C ha^{-1} yr^{-1} and 4.8 kg N ha^{-1} yr^{-1}. The difference in N yield between burned and reference watersheds was significant ($p<0.05$), but there was no significant difference in C yield (Fig. 12). In general, inorganic carbon was a small fraction of total dissolved carbon (accounting for <1%); therefore, my analysis focuses on DOC. TDN and DOC yield was positively correlated with average watershed slope ($r=0.4$, $p<0.01$). TDN yield was also positively correlated with the fraction of the watershed burned

(r=0.32, p<0.05), and the fraction burned with low to moderate severity fire (r=0.4, p<0.01). Yields were also positively correlated with stream flow (r=0.9, p<0.01).

Concentrations of DOC (mg L^{-1}) in stream samples were significantly higher in reference watersheds relative to burned watersheds for both Front Range fires (p<0.05) (Fig. 12). TDN concentration was significantly higher in burned watersheds in the Waldo Canyon area (p<0.05), but did not differ between reference and burned watersheds for the Hayman fire (Fig. 12). DOC concentration was negatively correlated with the fraction of the watershed burned (r= --0.66, p<0.01) (Fig. 13). TDN concentration was positively correlated with fraction burned (r=0.51, p<0.01) (Fig. 13).

For the Hayman fire, the stream C:N ratio was higher in the reference watershed (13.7 ± 8.04) relative to the burned watersheds (6.8 ± 4.25) (p<0.10), and significantly higher in the reference watersheds in the Waldo Canyon area (16.2 ± 14.9) relative to the burned watersheds (4.28 ± 3.05) (p<0.05). Stream SUVA did not vary with fire history in the Hayman fire area, but was significantly higher in the unburned watersheds in the Waldo Canyon fire area relative to the unburned watersheds (p<0.01). The dissolved C:N ratio was negatively correlated with fraction burned (r= -0.58, p<0.01) and with fraction low severity burn (r=0.5, p<0.01). SUVA was also negatively correlated with fraction burned (r= -0.28, p<0.05) and with fraction low severity burn (r= -0.58, p<0.01).

5. DISCUSSION

5.1 Total Carbon

Both ecosystem type and fire history were determinant of the size of carbon pools. Total ecosystem carbon was approximately 53% lower in the undisturbed Ponderosa pine forest plots relative to the undisturbed Lodgepole pine forest (Fig. 4). This was primarily due to the significant difference in soil C stocks; the montane ecosystem had ~70% lower total soil C and 95% lower course fraction organic content than the subalpine soils. Thus, there are clear differences between the two forest types. In the more mesic subalpine environment, there was higher C sequestration in soils, including higher soil charcoal content.

Within both ecosystems, fire affected C stocks, though the effect was larger in the subalpine Routt National Forest. Disturbed plots in the montane ecosystem had on average 52% less total carbon than undisturbed plots, but there was large variation between plots, such that the differences were not statistically significant (Fig. 4). The variation in total ecosystem carbon in the Hayman fire area was largely due to the reduction in aboveground biomass (~80% decrease relative to unburned plots). There was no significant difference in total soil C across fire history in the Hayman fire area. The fact that the total soil C pool did not differ across fire history in the Hayman area, but the % fine fraction soil C was ~50% lower in burned plots, was the result of changes in soil structure leading to increased bulk density in the burned soils. Bulk density of burned soils in the Hayman fire area was ~25% higher relative to unburned soils ($p < 0.10$). This is likely caused collapse of organo-mineral aggregates as a result of fire (Certini 2005).

Buma et al. (2014) found a similar decrease in total ecosystem C stocks of 58% relative to reference plots in the Routt National Forest, which was significant ($p < 0.05$). Comparing total soil carbon (43.2 ± 14.3 Mg C ha^{-1}) found by Buma et al. (2014) in

burned plots in the Hinman fire area with my result of 31.7 ± 14.4 Mg C ha^{-1} showed that there was no significant difference in soil C between sampling dates. This suggests that the use of data from Buma et al. (2014) for aboveground C stocks in the Routt National Forest plots was reasonable. The difference in ecosystem carbon between burned and undisturbed ecosystems in the Routt Hinman area was the result of a loss of aboveground biomass (61% reduction) as well as soil C (41% reduction, due to the near-complete loss of the soil organic layer) (Buma et al. 2014). This difference in the effect of fire on ecosystem carbon may be partially explained by the fact that under undisturbed conditions, soil C made up a larger proportion of total ecosystem C in the Lodgepole pine forest (~22%) than the Ponderosa pine forest (~14%).

Total ecosystem C storage had not recovered in either location. However, the rate of accumulation of soil carbon greater in the subalpine Routt Hinman fire area relative to the Hayman fire area ($p<0.1$). Assuming that both fires resulted in near-complete loss of soil C in the top 10 cm, an approximate post-fire rate of soil C accumulation (g C yr^{-1}) was able to be calculated by dividing average total soil C in each burn area (excluding coarse fraction char) by the time since fire. It is probably not true that one hundred percent of soil carbon was oxidized in these fires, but the fact that there was virtually no organic soil even thirteen years after fire suggests that this is a reasonable assumption. Thus, given that the top 10 cm of soil was the most affected by fire, it was useful to consider C accumulation in the surface soil to make a comparison in recovery rate between ecosystems. The soil C stock (top 10 cm) in the Hayman fire area recovered at a rate of approximately 1.14 Mg C ha^{-1} yr^{-1}, while the rate of recovery in the Routt Hinman fire area was approximately 2.25 Mg C ha^{-1} yr^{-1} ($p<0.10$). This difference was due to the

fact that tree recolonization was much more rapid in the Routt Hinman fire area (Fig. 2).

Ten years post-disturbance, Aspen had begun to reestablish where root systems were not

destroyed, and Lodgepole pine saplings had germinated from serotinous cones. In

contrast, there were no saplings in the Hayman burn plots.

Because Ponderosa pine lack cone serotiny, high-severity fire destroyed seed

reserves, contributing to slow tree recolonization (Rhoades 2011). Regeneration thus

depended on seeds spreading from nearby undisturbed forest, and favorable conditions

for seedling establishment (Dore et al. 2012). Law et al. (2003) found that water stress in

young trees slowed regrowth of Ponderosa pine; reestablishment of pine stands took 10-

20 years. In the Hayman fire area, grasses, forbs, and shrubs had returned to prefire

conditions, consistent with results from Rhoades et al. (2011). There was consistently

(though not significantly) greater grass, forb, and shrub carbon in the disturbed plots

relative to the reference plots. It is possible that the growth of grass, forbs, and shrubs

hindered the establishment of tree seedlings by outcompeting for limited water and soil

resources (Putz and Canham 1992). In fact, an eventual return to prefire conditions is not

necessarily a given; studies have shown that severe fire in Ponderosa pine forest can

result in a shift in vegetation type to grassland or shrubland, resulting in a net loss of C

(Dore et al. 2012).

Another potential barrier to tree recolonization in the Hayman fire area was

nitrogen availability. Due to the lack of moisture and slow rate of decomposition of plant

material, Ponderosa pine forests tends to be nitrogen limited (Covington et al. 1992). A

reduction in N following fire could exacerbate N limitation in these forests and hinder

regrowth. In the Hayman plots, soil %N was approximately 47% lower and extract TDN

28% lower in burned plots relative to reference plots, suggesting that fire resulted in a loss of available soil nitrogen; these differences were significant ($p<0.05$). This likely occurred through a combination of different processes. High-intensity fire volatilized nitrogen from soils and organic matter, causing a direct loss (e.g. González-Pérez et al. 2004, Ice et al. 2004). It is also likely that in some areas, partial combustion of plant material released N to available forms (i.e. ammonium) (Covington et al. 1992). Then, with reduced plant N demand and reduced allelopathic inhibition of nitrifying bacteria from Ponderosa pine (Lodhi and Killingbeck 1980), microbial N processing was accelerated. High nitrification rates may have resulted in conversion of ammonium to nitrate and subsequent losses to aquatic systems (Covington et al. 1992). These processes could explain the loss of available soil N, which may have contributed to slow regrowth in the Hayman fire area. Interestingly, soil %N was also significantly lower in burned soils in the Routt National Forest relative to reference soils (~55%) ($p<0.05$). However, there was ~126% higher soil N in the subalpine soils than the montane soils, suggesting that the Lodgepole pine forest naturally had greater N availability under undisturbed conditions, and may have been less sensitive to losses.

It is worth noting that there were enough clear differences in ecosystem and watershed characteristics to preclude a comparison between the Waldo Canyon burn plots and the Hayman area reference plots. The Dry Creek watershed was steeper, more densely vegetated, and moister than the Painted Rocks watershed, suggesting that the undisturbed conditions of the ecosystem were not equivalent. However, there were some differences in C pools that merit consideration. The Dry Creek plots had consistently higher total ecosystem C and aboveground biomass relative to the Pine Creek watershed,

though on par with the Fourmile Creek watershed, and significantly higher soil % C than the Hayman burn sites ($p<0.05$). This was largely due to the difference in fire severity; in the Waldo Canyon plots, there was less than total loss of soil organic matter and tree cover, as well as rapid recovery of forb and shrub carbon. Given the low severity of the fire disturbance in the Dry Creek watershed, there were fewer barriers to recovery of vegetation, allowing for faster regrowth and greater additions of C to the soil.

5.2 Soil

The results of the incubation experiment show microbial activity in a laboratory setting over time. Various factors, including substrate quantity and quality and environmental conditions, control rates of microbial decomposition of fine fraction soil organic matter (Fig. 14). Normalizing respiration results to soil C quantity provided a measure of carbon quality, or bioavailability, with the caveat that soil moisture did vary between plots. The effect of differential microbial community was assumed to be minimal relative to the effect of substrate quality and physical environment (Fierer et al. 2009). Microbial communities tend to be fairly similar, although they vary somewhat with the overlying vegetation (Fierer et al. 2009). Ayres et al (2009) found that in forest soils, microbial communities are slightly adapted to the types of litter they encounter; this "home field advantage" accounts for ~8% difference in decomposition rates (Ayres et al. 2009). Therefore, I focus on C quantity and quality and soil moisture as the primary drivers of differences in rates of microbial respiration. Indirect drivers of microbial activity include abundance and type of vegetation, soil nutrients, and soil physical properties which determine soil moisture, all of which were influenced by fire (Fig. 14). I

examine how these factors vary across ecosystem type and fire history. For the purposes of clarity, I will refer to the microbial activity metric of g C-CO_2 g^{-1} soil C as 'bioavailability', although it was not a direct measure of soil organic matter chemical structure or quality.

It is worth noting that the overall quality of the soil organic pool is a property of its composition. The organic pool is thought to consist of three general fractions: 1. Labile C pool, mainly from leaf litter and microbial biomass, 2. Intermediate C pool, mainly from woody fragments and litter, with a turnover time of years to decades, and 3. Passive C pool, made up of recalcitrant compounds with a turnover time of centuries to millennia (González-Pérez et al. 2004, Knicker 2007). Figure 15 shows inputs of organic matter and soil processes, which determine the size of soil C fractions. The relative proportions of the active, intermediate, and passive soil C pools determined the relative rate of microbial respiration per gram of total soil C.

5.2.1 Soil Physical Properties

Soil moisture significantly varied with ecosystem type. It was ~136% higher in soils from the subalpine ecosystem relative to soils from the montane ecosystem, largely due to the differences in precipitation and soil organic matter (affecting water holding capacity) (Brais et al. 2005). In addition, fire-induced changes in hydrology were evident in the Front Range plots (though not in the Routt National Forest). Soil moisture was ~40% lower in burned plots relative to unburned plots in the Hayman fire area ($p<0.1$). As expected, total soil respiration was positively correlated with soil moisture, although the relationship was nonlinear. This indicates that most of the soils were moisture-limited. Thin moisture films on soil surfaces limits diffusion of substrates to microbes,

reducing rates of decomposition (Stark and Firestone 1995). Given that few of the soil samples exceeded 30% moisture, it is unlikely that microbial respiration was limited by oxygen availability. When transformed to be normally distributed, soil moisture accounted for ~20% of the variation in respiration rate. Thus, moisture was a weaker determinant of microbial activity than soil C quantity and quality. When C quantity was controlled for, the microbial decomposition rate per gram soil C was negatively related to soil moisture, again non-linearly (Fig. 10A). This was likely driven by differences in ecosystem type. While soil moisture was lower and soil C bioavailability was higher in the montane ecosystem relative to the subalpine ecosystem, within each set of soils there was no relationship between soil moisture and bioavailability.

Bulk density, which decreases with higher soil moisture, organic matter content, and porosity (Certini 2005), was negatively correlated with total respiration, and positively related to soil C bioavailability. However, these relationships were largely the result of ecosystem differences. For the soils from the Routt National Forest, there was higher overall soil organic content, higher soil moisture, higher respiration and lower soil C bioavailability relative to soils from the Front Range sites. But within each set of soils, respiration and bioavailability were not significantly correlated with bulk density.

5.2.2 Microbial Respiration

Relative soil respiration (mg C-CO$_2$ respired over 7 weeks), was ~40% lower in disturbed plots within the Routt National Forest relative to reference plots ($p<0.05$) but did not differ with fire history in the Hayman fire area (Fig. 8A). It was also ~42% lower overall in the montane ecosystem relative to the subalpine ecosystem. This pattern is due to differences in the quantity of soil C in each plot. As expected, soil respiration was

positively correlated with soil carbon, including total soil carbon and %C of fine fraction soil ($p < 0.05$). With more organic matter in the soil, the microbes were more active, suggesting that microbes in these soils were C-limited.

Respiration was also positively correlated with TDN of soil extracts and %N of fine fraction soil ($p < 0.05$). Given that organic matter also contains nitrogen, it was expected that soil respiration would also increase with soil nitrogen. In addition, Kaye and Hart (1997) show that microorganisms utilize mineral nitrogen and may be N-limited in certain cases; therefore, soil nitrogen availability may have directly influenced rates of microbial activity. There was a weak negative relationship ($p < 0.15$) between respiration and nitrate from soil extracts, however, and a positive relationship with extract organic N ($p < 0.01$). This suggests that microbial activity was dependent on organic matter availability more than inorganic N. Further, Figure 6 shows that in the Hayman fire area plots, where relative respiration was low, inorganic N greatly exceeded soil organic N. Microbial respiration was also positively associated with mineral nutrients, including potassium, magnesium and calcium ($p < 0.05$) (see Appendix I for full list of correlations). Since higher concentrations of base cations contribute to growth of vegetation (Knicker 2007), plots with more available soil nutrients tended to have greater soil organic content.

Soil respiration was also positively related with total ecosystem C ($p < 0.05$), including aboveground biomass C ($p < 0.05$) and CWD ($p < 0.10$). The best predictor for soil respiration was % woody material of course fraction soil (accounting for ~30% of the variation in respiration rates). Thus, the content of organic material in the soil was the major determinant of the rate of microbial activity. Various studies of soil respiration in forest ecosystems have shown similar results. Buchman (2000) found that the

experimental removal of litter and organic layers from Norway spruce forest soils reduced respiration rates by ~40%. In addition, Marañon-Jimenez et al. (2011) found that soil respiration in a recently burned Mediterranean mountain ecosystem was highest when all snags were cut down and branches lopped off and left on the ground (increasing CWD), and that soil respiration was positively correlated with green herbaceous cover. Within the Front Range sites, respiration was strongly correlated with forb and shrub carbon (r>0.7, p<0.01).Therefore, soil respiration was positively associated with organic carbon, which depended on both fire history and ecosystem type. Respiration was not correlated with soil C bioavailability or soil C:N among all soil samples, suggesting that C quantity was the more important determinant of microbial activity. This suggests that soil C bioavailability would not have a major effect on the rate of soil respiration. However, within the Front Range plots, there was a positive relationship between respiration and the proxy for soil C bioavailability. Where total soil C was low, C quality had a larger effect on the overall respiration rate.

While this study could not estimate actual rates of CO_2 emission from soil, it did provide relative microbial respiration rates. Other studies have considered how actual rates of soil respiration vary with fire, providing some support for my findings. Dore et al. (2008) found a 30% decrease in total ecosystem respiration in an Arizona Ponderosa pine forest ten years after a severe fire using eddy covariance methodology. This was due to the loss of organic matter, similar to what was seen in the Routt National Forest. Other studies have found increases in soil respiration following fire, but generally on a shorter timescale, i.e. within several months of a fire (e.g. Wuthrich et al. 2002). Depending on the plant community and fire severity, fire can break down litter and woody material to

biodegradable forms, although in pine forests it is more likely to produce black carbon and other forms of C resistant to degradation (González-Pérez et al. 2004). Respiration also depends on environmental factors, such as changes in soil moisture and temperature following fire. Whatever the effect on soil respiration, the loss of live vegetation following a stand-replacing fire generally results in a drastic decrease in GPP, making the ecosystem a net source of carbon for years to decades (Dore et al. 2008, 2012). It is probable that this was the case in the in the Hayman fire area, given that soil respiration in burned plots did not decrease relative to reference plots, and there were no saplings in the burned plots contributing to NPP. Further study is needed to understand the net carbon balance in both ecosystems.

5.2.3 Soil Carbon Bioavailability

The proxy for relative soil C bioavailability (mg C-CO$_2$ g^{-1} soil C) was higher in burned plots in the Hayman fire area relative to reference plots (~44%) (Fig. 8B). Relative to the subalpine ecosystem, bioavailability was also ~44% higher in the montane ecosystem relative to the subalpine ecosystem. Overall, this difference appeared to be related to additions of complex organic C to the soil. Bioavailability did not differ significantly with fire history in the Routt National Forest; however, there was greater variability in soil C bioavailability in the burned plots within the Routt National Forest (Fig. 8B). Fire does not burn homogenously, usually representing a range of intensity within the area it affects (Hatten et al. 2005), resulting in increased soil heterogeneity as seen in the Routt/ Hinman fire area.

Given that the Hayman and Hinman fires destroyed the live forest cover as well as the organic soil layer, the measured soil carbon thirteen years post-fire was from several

sources: mineral soil C left after the fire, C additions from aboveground biomass that was not fully combusted but left as CWD and snags, C additions from recovering vegetation, and microbial biomass (Fig. 15). Depending on the duration of the fire and the soil temperatures reached, fire has a varied effect on the composition of soil organic matter (González-Pérez et al. 2004). Most studies show an increase in aromaticity and a decrease in biodegradability of soil carbon following severe fire in pine forests, resulting from incomplete oxidation of organic materials (González-Pérez et al. 2004, Olefeldt et al. 2013). Therefore, if the largest fraction of soil C was the remnant pool of pyrogenic compounds, the results showing higher soil C bioavailability in the burned Front Range plots were unexpected (Fig. 5B). This suggests that within the first decade after a stand-replacing fire in a Ponderosa pine forest, new additions of C to the soil increased the overall bioavailability of the soil organic matter, thus masking the direct effect of fire on soil C quality. This occurred despite the lack of tree regeneration in the Hayman fire area.

Soil C bioavailability was negatively correlated with total soil C, soil % woody material, fine fraction soil %C and %N, extract DOC and TDN and organic N ($p<0.05$). It appears that the soil C quantity was associated with the proportion of complex, less bioavailable organic compounds in the soil, and soil N increased with soil C (Fig. 9). Since soil C tended to be higher (and bioavailability lower) in reference plots relative to burn plots, it is unlikely that this correlation was the result of a direct effect of fire on the soil C pool. Rather, in the plots with more total vegetation and more trees, and thus more inputs of complex organic C to the soil, the soil C pool consisted of a smaller proportion of labile compounds. This appeared to be the case in the Front Range plots, where the dominant vegetation in the burned plots were grass, forbs, and succulents, which had a

lower C:N ratio than pine litter (Table 3). The reintroduction of "understory" vegetation such as grasses, forbs, and succulents within the first several years post-fire (Rhoades 2011) allowed the total soil C content to recover rapidly. This was possible in the montane Ponderosa ecosystem because soil C storage was low even in a mature forest, accounting for only 14% of total ecosystem C in the reference plots (Fig. 4). Though total soil C was the same across fire history in the montane ecosystem, the soils within the reference plots were less dense and consisted of a larger % woody material and soil C content, and lower bioavailability of the soil C pool. In the burn plots, there was rapid C turnover from grass and forb organic material and potentially greater microbial biomass.

Further, within the montane plots, soil C bioavailability was weakly negatively associated with litter Mg C ha^{-1}($p<0.15$) and weakly positively associated with shrub Mg C ha^{-1} ($p<0.15$), suggesting that C inputs to soil from pine litter were less bioavailable than inputs from understory vegetation. This makes sense, since the C:N ratio of leaves from M. mahogany and G oak (~20) was lower than that of pine litter (~70) (Table 3). Interestingly, however, within the montane plots soil C bioavailability was negatively correlated with grass Mg ha^{-1} ($p<0.1$). This was unexpected based on the hypothesis that there was higher soil C bioavailability in plots with more grasses and shrubs and fewer trees. The pattern of decreasing bioavailability with increasing grass cover likely came about because microbial biomass contains more labile C than grass litter, and in the absence of plant litter, the primary source of soil organic matter is dead microbes (Fig.15). This was supported by the positive correlation ($r=0.73$, $p<0.01$) between soil C bioavailability and % ground cover of dirt/gravel within the Hayman area plots.

Among all study plots, soil C bioavailability was also negatively associated with aboveground biomass and total ecosystem C (Fig. 10). This supports the hypothesis that in plots with forest cover, there were larger additions of complex, less biodegradable organic matter to the soil. This could help explain the difference in soil C bioavailability between the undisturbed montane Ponderosa pine forest and subalpine Lodgepole pine forest. Total ecosystem C was approximately 53% lower in the montane ecosystem compared with the subalpine ecosystem, primarily due to the difference in CWD (~87% lower in the montane forest) and in total soil C (~70% lower). The more mesic Lodgepole pine forest contained more carbon overall (Fig. 4), and a larger proportion of the carbon was stored in the soil rather than aboveground biomass. The result of greater C inputs to soil from CWD and vegetation in the subalpine forest was a smaller soil pool of labile C relative to the Ponderosa pine forest.

Ecosystem differences also resulted in a different response to fire in the Routt National Forest. Although the severity of the Hinman fire was similar to that of the Hayman fire, the quality of the soil organic matter was not significantly different between burned and unburned plots in the subalpine Routt forest. This was due to the input of C from tree regrowth in burned plots. Lodgepole pine can reproduce from serotinous cones opened by fire, and as a result, tree recolonization was much more rapid in the Routt Hinman fire area relative to the Hayman fire area (Fig. 2). Although aboveground biomass and soil C were significantly lower (~61% and ~41%, respectively) in the burned plots within the Routt National Forest relative to the unburned plots, the C inputs to the soil were from the same sources (i.e. Lodgepole pine). Therefore, the quality of soil organic matter did not differ significantly with fire history after 13 years of regrowth.

In addition, a remnant pool of aromatic compounds with low biodegradability might have remained after the fire (González-Pérez et al. 2004, Knicker 2007, Olefeldt et al. 2008), contributing to the low overall soil C bioavailability seen in the burned soils within the Routt National Forest. Given that the subalpine soil was relatively moist and contained a significantly larger carbon pool to begin with, the fire may have resulted in less than complete oxidation of soil organic matter, creating new C forms resistant to biological degradation (González-Pérez et al. 2004). However, the incubation experiment only showed the net rate of microbial decomposition per gram of fine fraction soil C; it did not allow a distinction between carbon inputs from Aspen and Lodgepole pine saplings and preexisting partially combusted soil organic matter.

The results of the incubation experiment showed that the % charcoal content of coarse fraction soil was a good predictor for soil C bioavailability (r= -0.428, p<0.05). Charcoal tends to be recalcitrant (e.g. DeLuca and Aplet 2008); thus, it was expected that with a larger pool of soil char, the proportion of labile soil C was lower. Course fraction soil char was significantly higher in the subalpine plots relative to the montane (p<0.05), likely contributing to the ecosystem difference in soil C bioavailability. Interestingly, however, the % charcoal content of course fraction soil did not vary with fire history in either the Routt Hinman or Hayman fire areas, suggesting that the fires did not in fact have a significant direct effect on the pool of recalcitrant soil C. These results are similar to Buma et al. (2014); they found no significant difference in total black carbon between burned and reference plots in the Routt Hinman fire area, including soil fine fraction and course fraction and aboveground char. Other research, reviewed by DeLuca and Aplet (2008), showed that due to a long history of fire in forested ecosystems of the Colorado

Rockies, charcoal makes up a significant portion of soil C (15-20% in the top 10 cm) and is minimally affected by individual fire events.

Aboveground char did vary with fire history; there was no BC on CWD in any of the reference plots. BC on CWD appeared to be a good predictor of soil C bioavailability in both ecosystems (r>0.7, P<0.001) (Fig. 10E). BC on CWD might simply an indicator for recent fire history (DeLuca and Aplet 2008), which is related to soil C quality. However, BC on CWD was still a good predictor for soil C bioavailability even when ecosystem type and fire history were controlled for. Perhaps an outer "skin" of charred material on felled logs and branches slowed decomposition of CWD, which is less bioavailable than other sources of C due to the high lignin content of woody material (Brais et al. 2005). CWD in forest ecosystems is important as a source of soil organic matter and for nutrient storage (Tinker and Knight 2000). However, charred organic material tends to have reduced biodegradability and solubility (González-Pérez et al. 2004), potentially limiting microbial activity and slowing incorporation of CWD into soil. In the absence of C additions from CWD, the soil C pool would likely represent a larger proportion of labile C from grasses/forbs and microbial biomass. Few studies have researched the relationship between aboveground char production and breakdown of CWD and snags; however, Tinker and Knight (2000) also found an outer shell of charcoal on otherwise unburned logs in Wyoming Lodgepole pine forests.

5.2.4 Soil C:N Ratio

While the incubation experiment provided a proxy of soil C bioavailability, the C:N ratio for soils and soil extracts was a direct measure of bioavailability (though it accounted for only one aspect of C quality). Overall, the soil C:N ratio was a good

predictor for the soil C bioavailability proxy, as expected (r= –0.4, p<0.001) (Fig. 9). The same was true for the extract DOC:TDN (Fig. 9). The ratios appear to be determined by the same factors that correlate with the bioavailability proxy. With higher total ecosystem C, aboveground biomass C, and soil C, there was more soil organic matter and a higher C:N ratio. Inputs of organic matter from trees (i.e. pine litter and woody material) had a higher C:N ratio than inputs from grasses, forbs, or shrub leaves (Table 3), or microbial biomass (Cleveland and Liptzin 2007). Thus, the forested plots had a smaller proportion of labile soil C relative to the Hayman burned plots. The extracted C:N ratio was higher overall in the subalpine relative to the montane soils, reflective of the difference in the vegetative community and total ecosystem carbon (Fig. 5). Interestingly, the extracted C:N was significantly lower for burned soils in both ecosystems (p<0.05), suggesting that there was more available labile organic matter in burned soils (or a greater proportion of inorganic N within SOM). On the other hand, the C:N of reference soils only exceeded that of burned soils in the Hayman fire area. It was expected that the soil C:N would not vary with fire history in the Routt Hinman fire area, given the presence of live forest cover in both burned and unburned plots and the fact that the proxy for soil C bioavailability did not depend on fire history in the subalpine forest.

Overall, stepwise linear models showed that the best sample-level predictors for bioavailability were: soil %N, soil %C, soil C:N, and extract Ca^+ (R^2=51.6%, p<0.01), although %N and %C co-varied. Therefore, both the quantity of soil organic matter and the C:N ratio were indicative of the overall quality of soil carbon. The best plot-level predictors were: total soil C and BC on CWD (R^2=62.43%, p<0.05), which did not covary.

5.3 Watershed Hydrology and Stream Chemistry

5.3.1 Hydrology

Stream sampling and GIS analysis facilitated a comparison of hydrologic processes and lateral exports of C and N between burned and reference watersheds in the Central Colorado study area; the same analysis was not conducted in the Routt National Forest. Water export varied with fire history, indicating that the Hayman and Waldo Canyon fires resulted in lasting changes in hydrology. Fraction of precipitation exported, calculated as stream discharge normalized to watershed area and divided by precipitation, was more than twenty times higher in the Hayman burned watersheds relative to the unburned watershed, and more than twice as high in the Waldo Canyon burned watersheds relative to the unburned watersheds (Fig. 11). This clear pattern suggests that water yield increased dramatically after fire and remained elevated for at least three years in the Waldo Canyon watersheds, and thirteen years in the Hayman watersheds.

Fire-induced changes in canopy structure likely contributed to increased water exports. This is supported by the fact that the increase in water yield was more dramatic for the Hayman fire where there was greater loss of forest cover. Moody and Martin (2001) found similar results in mountainous watersheds of Colorado. In the burned watersheds, the loss of tree cover led to decreased interception and infiltration, higher runoff rates and increased peak discharge in streams (Moody and Martin 2001). Changes in soil physical properties, including depleted soil organic matter and increased bulk density, also contributed to changes in flow paths in these watersheds by reducing soil permeability. Soil hydrophobicity may have contributed to reduced infiltration as well, resulting in overland flow (Ice et al. 2004). However, it has been shown that soil

hydrophobicity tends to weaken within one year after fire in Ponderosa pine forests (Knicker 2007). Since my results are from >3 years post-fire, it is likely that hydrophobicity accounted for less of the difference in water yield between burned and unburned watersheds than changes to flow paths resulting from the loss of vegetation.

Indeed, the recovery of hydrologic processes has been linked with post-fire regrowth (Cerdá and Doerr 2005). In a severely burned pine forest in Spain, Cerdá and Doerr (2005) found elevated runoff and erosion immediately after fire, which returned to pre-fire levels with the regrowth of herbaceous cover, within three years. However, grasses and herbaceous cover had largely regenerated in both the Hayman and Waldo Canyon burn areas at the time of sampling. This indicates that there may have been other factors contributing to the observed differences in water yield between burned and reference watersheds. The precipitation regime was comparable across the region; precipitation in each watershed deviated on average <5% from the mean of 0.15 m in June and July 2015. However, other differences in watershed characteristics (i.e. slope) contributed to the observed pattern. Fraction of precipitation exported was positively correlated with mean watershed slope (r=0.536, p<0.001), and a couple of the steepest watersheds included in the study (e.g. Dry Creek) were burned. Nevertheless, water export is positively correlated with fire extent, suggesting that both fire history and watershed characteristics influenced flow paths.

5.3.2 Lateral Exports

The implications of increased water yield include increased erosion and leaching. These effects tend to be highest within the first months after fire, but can account for significant losses of soil nutrients and organic matter (e.g. Ice et al. 2004, Moody and

Martin 2001, Smith et al 2011, Murphy et al. 2006, Rhoades 2011). Losses of soil and soil nutrients, potentially exceeding supply, could impact the recovery trajectory of the ecosystem, with long-term implications for the ecosystem carbon budget (Kranabetter et al. 2015). In fact, nutrient export did vary with fire history in the Hayman and Waldo Canyon watersheds. Yields of C and N (g m^{-2} yr^{-1}) from the Hayman reference watershed were ~86% and 92% lower, respectively, than from burned watersheds (Fig. 12). For the Waldo Canyon fire, total nitrogen yield was ~75% lower in reference watersheds relative to burned watersheds, although there was no significant difference in C yield (Fig. 12). This indicates that nitrogen exports remained elevated in burned areas, with implications for terrestrial N availability. DOC exports also increased after fire in the Hayman fire area, where there was a greater difference in water yield between burned and reference watersheds. This has implications for C fluxes in aquatic ecosystems, which is a significant C source to the atmosphere (e.g. Raymond et al. 2013, Aufdenkampe et al. 2011). However, stream C exports were small compared with total soil C accumulation. Extrapolating from summer stream measurements, only ~0.09% of total soil C from burned watersheds in the Hayman area watersheds was exported to streams in 2015.

Yields of carbon and nitrogen were highly dependent on flow, as expected. With more water exported from these watersheds, DOC and TDN yields increased (r<0.9, p<0.001). In addition, concentrations of DOC and TDN (mg L^{-1}) in stream samples varied with fire history (Fig 12). This indicates that fire impacted the availability of C and N for export as well as water yield. Figure 13 shows that DOC concentration tended to decrease with greater fraction burned (r= -0.66, p<0.01). With reduced plant cover and loss of soil C through combustion, there was less organic soil C available for export to

streams. On the other hand, TDN concentration increased with fire extent and fraction low severity burn (Fig. 13) (r=0.722, p<0.01), suggesting that soil N availability increased as a result of low severity fire. This is consistent with various studies which showed increased stream-water nitrate after fire (e.g. Rhoades 2011, Murphy et al. 2006). Rhoades et al. (2011) accelerated microbial N processing in the Hayman fire area, due to increased soil temperature and pH, reduced plant demand, and increased soil N availability from the combustion of soil N reservoirs. This resulted in increased leaching. Other studies have also found increased nitrification after fire. Reduced competition with plants may allow autotrophic nitrifiers to convert NH_4^+ to NO_3^- more rapidly (Kaye and Hart 1997, Covington et al. 1992, Lodhi and Killingbeck 1980). This leads to increased N losses to streams, since NO_3^- tends to be more mobile than other forms (Certini 2005).

In addition, these results show that burn severity had an impact on soil N availability and lateral exports. The fraction of the watershed burned with high-severity fire was not correlated with stream N concentration or yield (r<0.1), but low-severity fire was positively correlated with TDN concentration (Fig. 13). Covington et al. (1992) found that low-severity burning in Ponderosa pine forest resulted in a nitrogen- enriching effect, because partial combustion of organic matter released N tied up in complex organic molecules (Covington et al. 1992). However, high temperatures near the soil surface during severe burn likely resulted in direct volatilization of soil N, leading to greater losses (Ice et al. 2004). As a result, the stream N concentration was higher in watersheds burned with low severity. In Ponderosa pine forest, which tends to be severely N-limited (Covington et al. 1992), increased mineral N following low-severity fire could stimulate regrowth, while high-severity fire could hinder regrowth.

5.3.3 Stream C:N

The stream C:N ratio was negatively related to burn extent (r= -0.58, p<0.01) (Fig. 13), possibly because of increased inorganic N exports from burned watersheds. This pattern may also reflect differences in the C:N ratio of SOM between burned and reference watersheds. The dominant vegetation in burned areas (i.e. grasses and forbs) may have contributed organic material with a lower C:N ratio to soils, and, subsequently, to streams, relative to inputs from trees. This is consistent with the results for soil C bioavailability showing lower bioavailability in plots with greater tree cover. If the organic matter exported to streams had a lower C:N and was, perhaps, more biodegradable, this could affect downstream rates of microbial activity (Olefeldt 2013). However, aromaticity, another indicator for biodegradability of organic compounds, showed inconsistent results. Stream SUVA did not vary with fire history in the Hayman area, but was greater in Waldo Canyon reference streams relative to burned watersheds (p<0.01). Further, stream SUVA was negatively correlated with low severity burn (r= -0.581, p<0.001). It is possible that a decrease in aromatic soil organic compounds occurred in areas affected by low severity fire. The Waldo Canyon soils had high relative rates of respiration, ~75% greater than respiration in the Hayman burn plots, suggesting that rapid microbial decomposition of organic material may have reduced the proportion of aromatic organic compounds in the Waldo Canyon watersheds. Wuthrich et al. (2002) also found elevated soil respiration following low-intensity fire in a Norway spruce stand.

Interestingly, in both burned and reference plots the C:N ratio of soil extracts was significantly lower than the soil C:N ratio (Table 2) (p<0.05). This suggests that N-rich organic matter may have been selectively exported from these watersheds, or that there

was more soluble inorganic N relative to SOM. In both burned and reference Hayman watersheds, extract inorganic N was higher than extract organic N ($p<0.01$), accounting for >75% of total dissolved nitrogen (Fig. 6). Thus, inorganic N was the major component of the soil N pool in the Hayman plots, though there was no difference in the ratio of mineral to organic N across fire history. The ratio of inorganic and organic soil N also varied with ecosystem type. Extract inorganic N from the subalpine soils was ~66% lower, and extract organic N 200% higher, relative to the montane soils ($p<0.01$), likely because there was more soil organic matter overall in the subalpine Routt forest. Though total extracted N was greater in the subalpine soils, the montane soils had greater inorganic N; therefore, N availability may have been greater in the montane ecosystem.

5.4 Limitations

A number of assumptions have gone into this study. Firstly, it was assumed that reference plots accurately reflect pre-fire conditions for burned plots within the same region. This was supported by shared prefire community structure (from prior USFS mapping), climate conditions, and bedrock type (USFS Mapping, personal communication). However, given the soil heterogeneity seen in these plots (see Table 2 for standard deviation of soil properties and C stocks), there was substantial variation even within a small area. In addition, topography was not the same among study sites; slope and aspect ranged widely (Table 1). Thus, the reference watersheds represent examples of undisturbed montane Ponderosa pine- Douglas fir forest and undisturbed subalpine Lodgepole pine forest, but cannot be considered to show exactly the prefire conditions of the burned areas.

In addition, the incubation experiment included some uncertainty. The study design attempted to keep the same conditions for incubated soils by controlling for temperature, leaving the jars open to the air, and adding water each week to return soils to the moisture content when they were collected. However, studies have shown that laboratory conditions influence microbial activity. The regulated temperature (5 °C) was generally lower than summer field temperatures. Adding moisture on a weekly basis also likely created a rewetting effect (Fierer and Schimel 2002, Marañon-Jimenez et al. 2011). Drying-rewetting cycles cause a short-term pulse in C & N mineralization rates, either from the osmotic shock releasing labile organic matter from microbial biomass pools, or by breaking up soil aggregates, thus exposing previously inaccessible organic matter (Fierer and Schimel 2002). Marañon-Jimenez et al (2011) measured the strength of this rewetting effect, finding that it accounted for 51-87% of CO_2 emissions from soils within 24 hours of rewetting (in a field setting). As headspace sampling occurred within several hours of rewetting, the measured rates of CO_2 respiration were likely significantly elevated from baseline levels. In addition, rewetting had an observable effect on soil structure, reducing soil WHC and aeration. However, as all soils underwent the same treatment, a comparison of relative rates of respiration between soils was valid. Further, Fierer and Schimel (2002) showed that drying-rewetting frequency had a small net effect on average soil respiration rates (±10%) over a two-month incubation experiment.

Another caveat was that the terrestrial analysis, including soil collection, represented a snapshot in time. This limited conclusions about recovery pathways for these ecosystems somewhat, given that there was no data showing how soil C bioavailability and other factors may have changed over time. In addition, comparing

between sites assumed that there were no changes in C stocks or other factors in the time between when data was collected at each site. In the Routt Hinman fire area, the ecosystem carbon census (including measurements for aboveground biomass, vegetative cover, CWD and total ecosystem C) was conducted by Dr. Buma in 2011, while soil collection was done in 2015. Measurements of soil C from the 2011 and 2015 were not significantly different, suggesting that the use of data from Buma et al. (2014) was reasonable. Nevertheless, it is likely that the aboveground C measurements were fairly conservative. Personal observation showed that there was significant regrowth at the time of resampling (Brian Buma, personal communication).

All soil collection in both the Front Range and Routt plots, as well as the Front Range terrestrial carbon analyses, occurred within a month in summer 2015. Given the short time span of collection, it is unlikely that the difference in collection dates significantly affected ecosystem or soil C. Individual precipitation events could account for some differences in soil moisture; for instance, soil collection in the Fourmile watershed occurred during a rainstorm. These soils with elevated moisture could have demonstrated elevated rates of microbial activity. However, moisture was a weaker predictor of microbial activity than substrate quantity and quality, especially within ecosystem types.

Another limitation stems from the fact that my analysis was primarily focused on the effects of severe fire. Though I considered burn severity in comparing the effect of the Waldo Canyon and Hayman fires on hydrology and C and N exports, the terrestrial analysis was limited by the lack of reference data in the Waldo Canyon fire area. Numerous studies have found that the impacts of increasing fire intensity on ecosystem

nutrient cycling and recovery pathways are nonlinear; low-intensity fire tends to have a minimal effect on soil properties (e.g. Hatten et al. 2005, Wuthrich et al. 2002). Therefore, my findings for terrestrial C stocks and soil C bioavailability likely have little applicability for low to moderate fire severity or other types of ecosystems.

6. CONCLUSIONS

In general, these results demonstrate that changes in C stocks and soil processes persisted thirteen years post-fire in the Hayman and Routt/ Hinman areas. Carbon stocks were generally smaller in burned plots relative to unburned plots (with the notable exception of soil C in the Hayman fire area). In addition, there was accelerated C cycling in the Hayman fire plots, evidenced by high soil C bioavailability and increased lateral DOC exports. Given these factors, as well as the lack of tree regeneration in the Hayman plots, it is likely that estimates in the range of 100-200 years for a full recovery of C storage (Law et al. 2003) are applicable to the Hayman fire. This suggests that the montane Ponderosa pine forest was more severely impacted by fire than the subalpine forest, perhaps because it had a large proportion of nutrients stored in aboveground biomass (~76% of total ecosystem C; Fig.4) (Kranabetter et al. 2015). The overall C sequestration potential of the ecosystem may change if the effects of the disturbance exceed ecological resilience and trigger a lasting change in the plant community composition (Dore et al. 2012, McLauchlan et al. 2014). This is made more likely by the loss of soil nutrients, namely nitrogen, in soils affected by the Hayman fire. Due to the sensitivity of Ponderosa pine forest to severe disturbance shown in this study, a long-term

change in the ecosystem carbon balance is likely to occur with increasing fire frequency and intensity (Kranabetter et al. 2015, McLauchlan et al. 2014).

The subalpine Lodgepole pine forest appeared to be more resilient than the montane Ponderosa pine forest, showing greater tree regeneration (Fig. 2) and no change in soil C bioavailability between burned and reference soils (Fig 8). This was expected, as Lodgepole pine is adapted to infrequent crown fires (Graham and Jain 2005). Therefore, the response to severe disturbance was largely dependent on ecosystem type. A shift in the disturbance regime may have less of an effect on Lodgepole pine forests in the Western U.S., although the C sequestration potential could still be impacted if the frequency of fires increases such that the return interval is less than the time needed to fully recover forest C stocks. Though tree regeneration in the subalpine Routt/ Hinman forest was more rapid than in the montane forest (Fig. 2), the overall recovery time might still be similar between the two ecosystem types, since there was greater total C storage in the mature Lodgepole forest relative to the mature Ponderosa forest. Therefore, there is a potential for a reduction in C sequestration over the region's forests, creating a positive feedback with climate change. However, these conclusions are somewhat limited by the fact that field respiration measurements were not taken, and therefore the net ecosystem C balance could not be closed. Further study is needed to measure total soil respiration, as well as the stream CO_2 efflux to determine how much terrestrial C is released to the atmosphere versus stored in vegetation, soils, and stream sediments. Further study could also consider the nitrogen balance of the ecosystem by taking more comprehensive measurements of terrestrial N stocks and exports.

To attempt to get a sense for C accumulation in each ecosystem, an approximate soil C recovery rate (Mg C ha^{-1} yr^{-1}) was calculated (assuming all non-char soil C in the top 10 cm had accumulated post-fire). Soil C recovery was approximately twice as fast in the subalpine Routt Hinman forest than in the montane Hayman forest (p<0.1), evidencing a faster recovery rate. This was likely due to cone serotiny in Lodgepole pine, as well as greater moisture availability; the subalpine ecosystem received on average 57% more annual precipitation (Stevens 2012). As Ponderosa pine tends to be drought-limited in early stages of growth, because of competition for water in the top 20cm of soil, years with above-average precipitation may be necessary for seedlings to establish and eventually recolonize the full area of the burn scar (Law et al. 2003).

Regrowth of trees appeared to be the major factor determining soil C bioavailability across the study sites. In the montane study area, the C inputs from grasses and forbs resulted in a lower soil C:N ratio and higher bioavailability in burned plots relative to the undisturbed, forested plots. C inputs from regrowth of Lodgepole pine in the subalpine study area resulted in comparable C:N ratios and bioavailability in burned and reference plots. Therefore, the dominant vegetation appeared to be the primary determinant of the quality of soil C thirteen years post-fire; C inputs from regrowing vegetation masked the direct effects of fire on the soil C pool in both ecosystem types. Further research is necessary to better understand the factors determining rates of tree recolonization, and thus how different forest ecosystems will respond to increasing fire frequency in and intensity. The spatial distribution of different plant types with regard to the edges of the burn area could be mapped in the Hayman area over time, to focus on the recovery and resilience not only of C stocks but of the plant community. In addition,

2002 was a year with a number of severe fires across Colorado; comparisons among different ecosystem types could be made by studying plant communities and C and N stocks in a number of burn areas.

In general, C stocks were smaller in burned plots, likely resulting in reduced total soil respiration relative to reference soils (as substrate quantity was the primary determinant of microbial respiration rates). However, with a smaller quantity of soil C (as in the Hayman soils), soil C quality was a good predictor for relative respiration. Therefore, it is likely that with less tree cover, respiration was higher than NPP, making the burned areas a net source of carbon. I postulate that there is a threshold for regrowth of woody plants above which the ecosystem shifts to a net C sink, since photosynthesis would be higher and soil C bioavailability less. Determining what that threshold is in different ecosystems, and the factors that determine how long it takes for tree regeneration to reach that point, is important to understanding how a change in the fire regime will affect the regional C balance of the Rocky Mountain West.

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8. TABLES AND FIGURES

8.1 DATA TABLES

Table 1. Montane watersheds. Burn severity data is the fraction of the total watershed area burned with low, moderate, and high severity fire based on Monitoring Trends in Burn Severity dataset (MTBS.gov). *Indicates watersheds which included terrestrial C analysis. **Sampling of Beaver Creek and Wellington Creek was interrupted partway through the study period because of access issues. Beaver was replaced by Monument Creek, which was also unburned.

	Watershed Name	Area (km^2)	Average Slope (deg)	% Area Burned	Fraction low/ moderate severity burn	Fraction high severity burn
Hayman Fire 2002	Wigwam	66.6	16.7	41.3	0.15	0.19
	Pine*	9.4	17.4	60.7	0.20	0.36
	Fourmile*	20.6	13.3	88.6	0.23	0.59
Waldo Canyon 2012	Sand	2.9	9.67	94.8	0.67	0.12
	Dry*	1.2	25.4	65.1	0.50	0.07
Reference	Painted Rocks*	5.2	6.50	—	—	—
	Beaver**	42.7	11.7	—	—	—
	Monument**	15.8	15.5	—	—	—

Table 2. Mean and standard deviation of microbial respiration, soil properties and C stocks for the Front Range watersheds and Routt National Forest plots.

	Soil Respiration (mg C-CO2)	Soil C Bioavailability (mg C-CO2/ g soil C)	%C	C:N	C:N of extract	Bulk Density (g/cm³)	Soil % Moisture	Soil % charcoal	Soil % woody material	Total Soil C (Mg C/ ha)	BC on CWD (Mg C/ ha)	Grass (Mg C/ ha)	Above-ground Biomass (Mg C/ ha)	Total C (Mg/ ha)
Dry	89.1±25.9	95.9±31.0	2.83±0.67	20.2±1.76	6.05±1.42	1.23±0.004	12.5±0.87	0.15±0.18	0.33±0.07	18.3±4.81	0.64±0.19	0.004±0.002	33.1±19.6	59.2±19.9
Pine	46.3±13.4	67.8±24.2	1.56±0.74	20.4±2.16	3.55±1.01	1.34±0.16	4.52±0.89	0.08±0.07	0.55±0.48	13.4±7.26	0.15±0.20	0.35±0.35	0.0	27.3±11.9
Fourmile	55.3±9.31	72.3±41.6	2.80±2.13	23.9±4.37	5.27±2.30	1.23±0.05	6.84±1.64	0.06±0.09	0.06±0.09	16.8±13.2	0.72±0.65	0.25±0.17	37.3±46.8	80.7±60.5
Painted Rocks	53.0±14.3	48.5±23.5	4.38±3.51	24.5±3.08	8.86±3.45	0.96±0.17	9.42±1.81	0.17±0.18	1.21±0.74	16.3±8.81	0.0	0.15±0.15	92.6±83.6	113.6±75.8
Routt Reference	91.3±26.9	33.7±15.4	11.0±7.57	26.1±3.56	19.0±5.44	0.42±0.14	22.2±8.54	3.21±3.96	40.5±17.1	53.7±11.6	0.0	0.26±0.11	213.6±62.6	240.3±75.1
Routt Hinman	55.6±18.4	38.3±22.9	4.90±3.61	26.5±7.53	7.88±3.96	0.87±0.15	23.5±5.89	0.97±0.61	1.23±0.74	31.7±14.4	0.19±0.20	0.24±0.08	83.7±22.7	99.3±22.7

Table 3. %N, %C, and C:N of vegetation samples collected in Front Range watersheds at the time of soil collection. Shrubs include leaf and branch samples from Mountain mahogany and Gambel Oak.
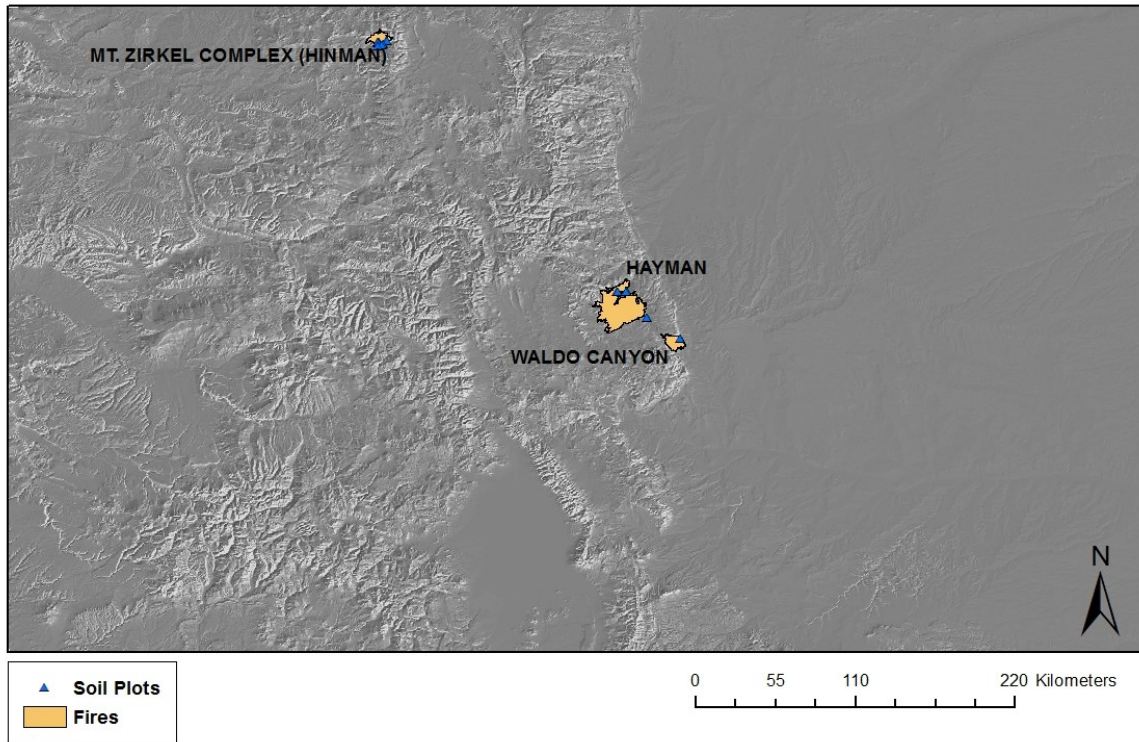
	Pine Litter	Grass	Forb	Shrub Leaves	Shrub Branches
%N	0.808	1.077	1.227	2.969	1.062
%C	48.43	43.51	45.87	49.11	47.78
C:N	69.91	47.13	43.62	19.53	62.87

Table 4. Calculated from weekly discharge measurements and analysis of stream samples. Includes all Front Range watersheds. Sample sizes: Sample sizes: Hayman n=23; Hayman reference n=8; Waldo Canyon n=21; Waldo Canyon reference n=9.

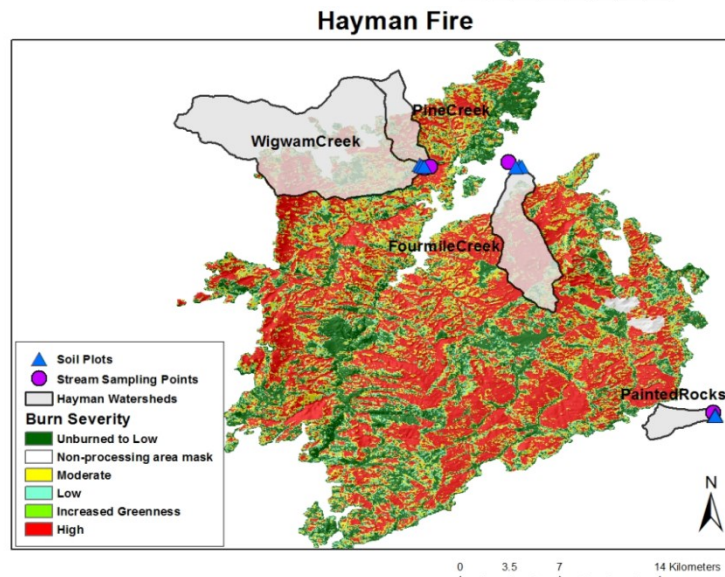|	Water Yield $(m^3\ ha^{-1}\ yr^{-1})$	C Yield $(kg\ ha^{-1}\ yr^{-1})$	N Yield $(kg\ ha^{-1}\ yr^{-1})$	SUVA	Stream C:N
Hayman	4505	13.9	4.1	3.2	6.8
Hayman Reference	259	1.9	0.187	3.16	13.7
Waldo Canyon	6054	14.9	4.8	2.16	4.28
Waldo Canyon Reference	2310	11.2	1.2	2.95	16.3

8.2 MAPS OF STUDY AREA

Map 1. Map of Colorado showing fire location and size. The Hinman fire burned in the Routt National Forest in Northwestern Colorado, near Steamboat Springs, CO. The Hayman and Waldo Canyon fires burned in Central Colorado, near Colorado Springs, CO. All maps were generated using GIS ArcMap 10.1 software.
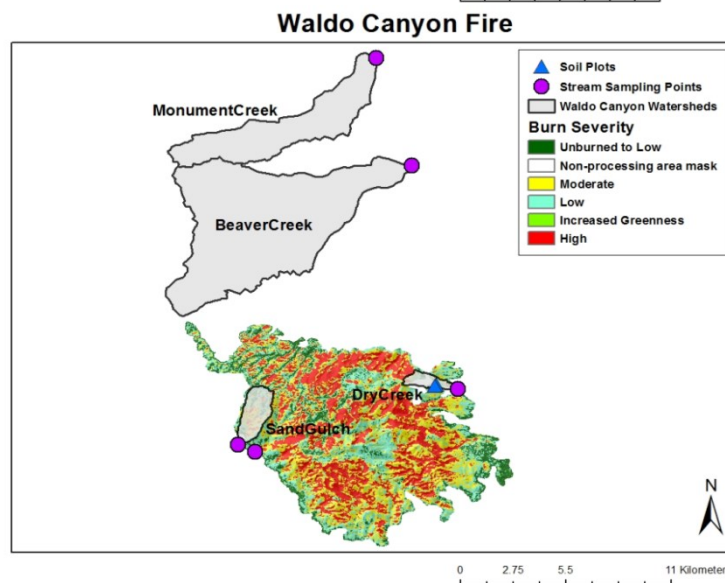
A.

Hinman Fire

- Soil Plots
- **Burn Severity**
  - Unburned to Low
  - Non-processing area mask
  - Moderate
  - Low
  - Increased Greenness
  - High

N

0   1.5   3   6 Kilometers
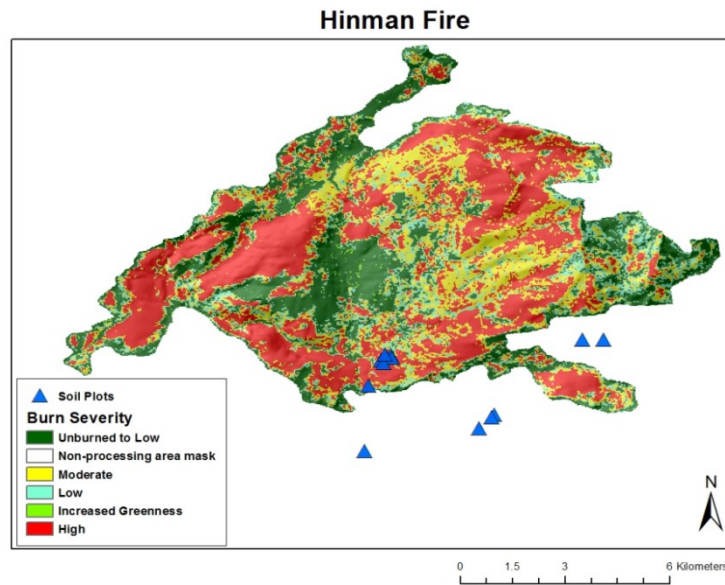
Map 2. Burn severity and location of terrestrial sampling plots for the **A)** Hinman, **B)** Hayman, and **C)** Waldo Canyon fires. The Hayman and Waldo Canyon fires also show stream sampling points and area of watersheds included in the stream analysis.

B.

Hayman Fire

PineCreek
WigwamCreek
FourmileCreek
PaintedRocks

- Soil Plots
- Stream Sampling Points
- Hayman Watersheds
- **Burn Severity**
  - Unburned to Low
  - Non-processing area mask
  - Moderate
  - Low
  - Increased Greenness
  - High

N

0   3.5   7   14 Kilometers

C.

Waldo Canyon Fire

MonumentCreek
BeaverCreek
DryCreek
SandGulch

- Soil Plots
- Stream Sampling Points
- Waldo Canyon Watersheds
- **Burn Severity**
  - Unburned to Low
  - Non-processing area mask
  - Moderate
  - Low
  - Increased Greenness
  - High

N

0   2.75   5.5   11 Kilometers

73

8.3 FIGURES AND DIAGRAMS

Figure 1. Schematic showing elevation and life zone of study sites.
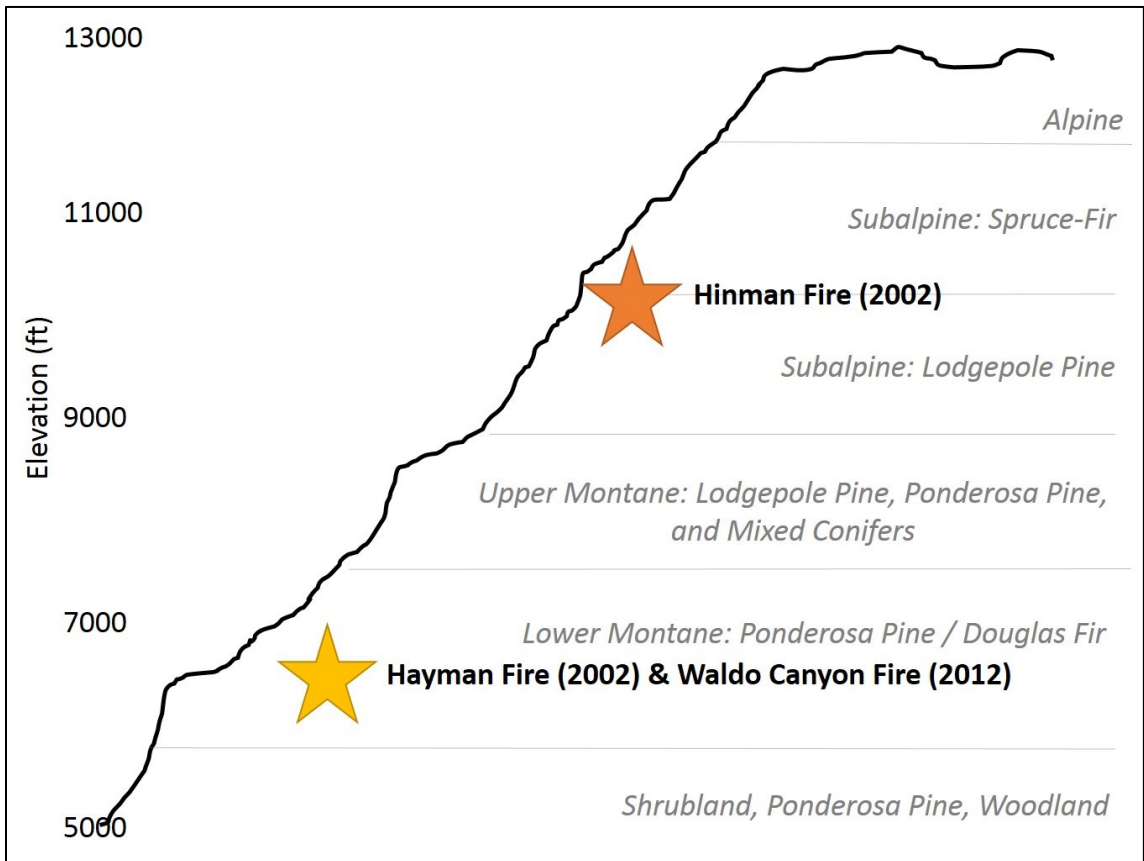
Figure 2. Photos of study sites. **A)** Pine Creek watershed, Hayman fire area. Taken June, 2015. **B)** Painted Rocks watershed, reference site near Hayman fire area. Taken June, 2015. Differential rate of tree regeneration is evident.

Figure 3. Sampling design for locating terrestrial plots according to hillslope position (in the Front Range watersheds) Crest plots were at the top of a hill, with no gravitational inflow of water or sediment. Midslope plots were along the steep part of the hillside. Toe slope plots were in the accumulation zone at the base of the hill, usually at the edge of the floodplain. Riparian zones were avoided in establishing terrestrial plots.
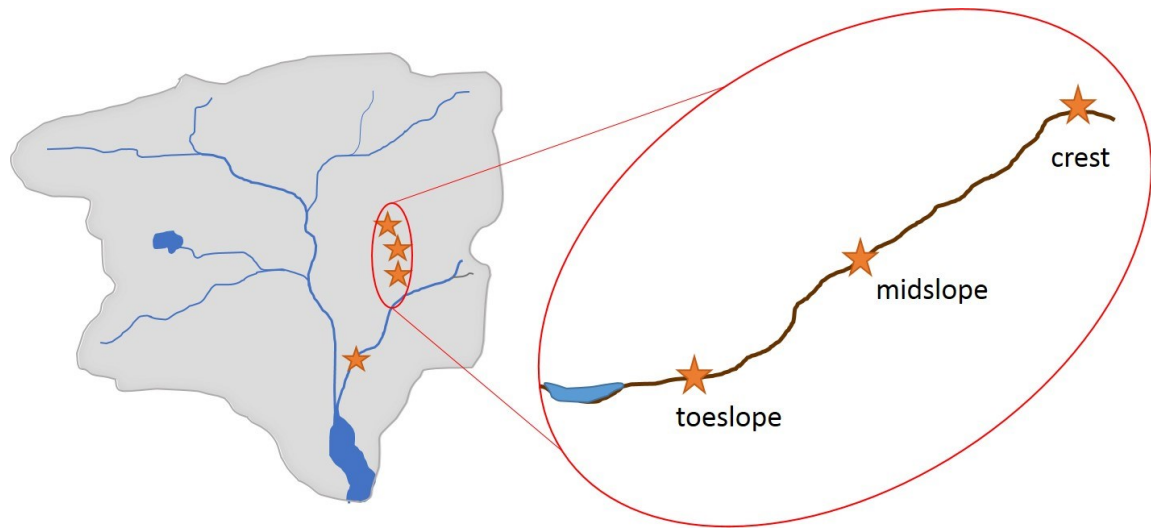
Figure 4. Ecosystem C stocks extrapolated from plot data, including total soil C (top 10 cm), aboveground biomass, and total ecosystem carbon (Mg C ha^{-1}). Different groups have a different sample size: Hayman fire (HF) n=6; Hayman Reference (HR) n=3; Routt Reference (RR) n=6; Routt Hinman fire (RF) n=6; Waldo Canyon fire (WC) n=2.
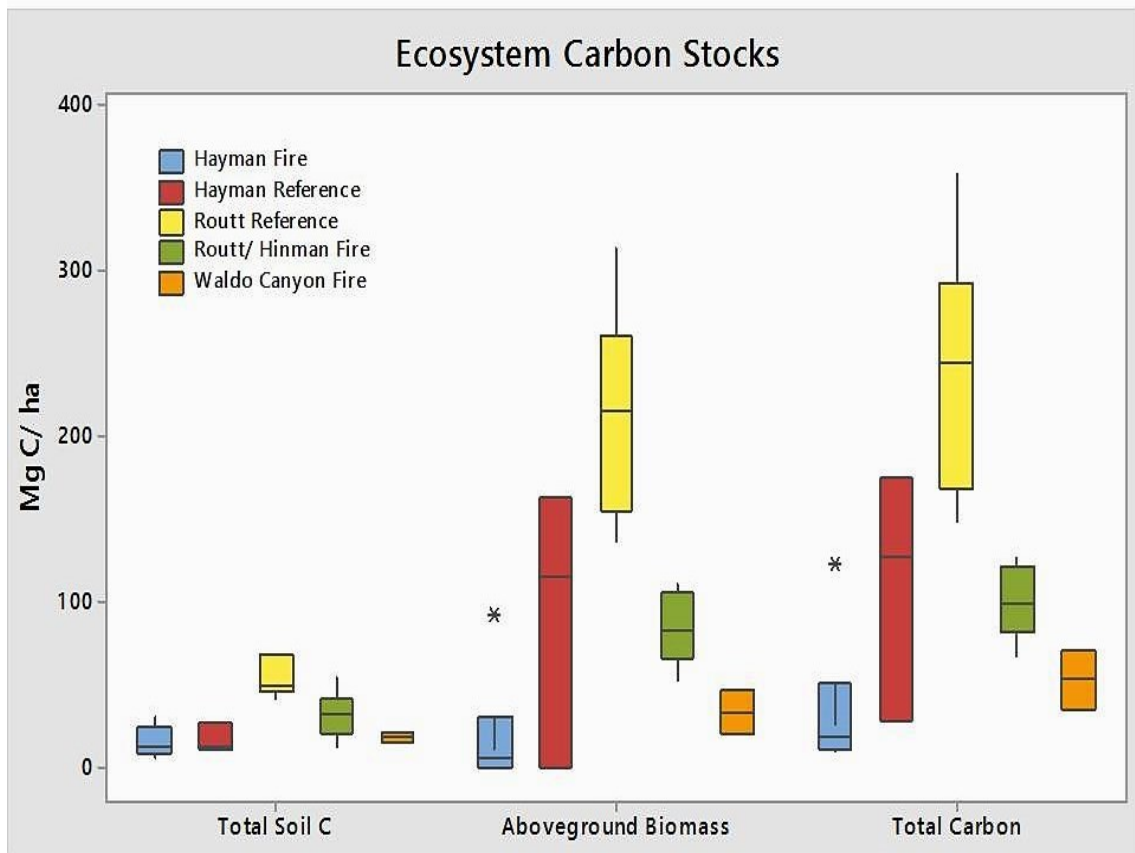
Figure 5. A) Soil C:N ratio, calculated from measurements of fraction soil % C and % N. **B)** DOC: TDN ratio of soil extracts. Sample sizes: HF n=18; HR n=14; RR n=18; RF n=19; WC n=6.
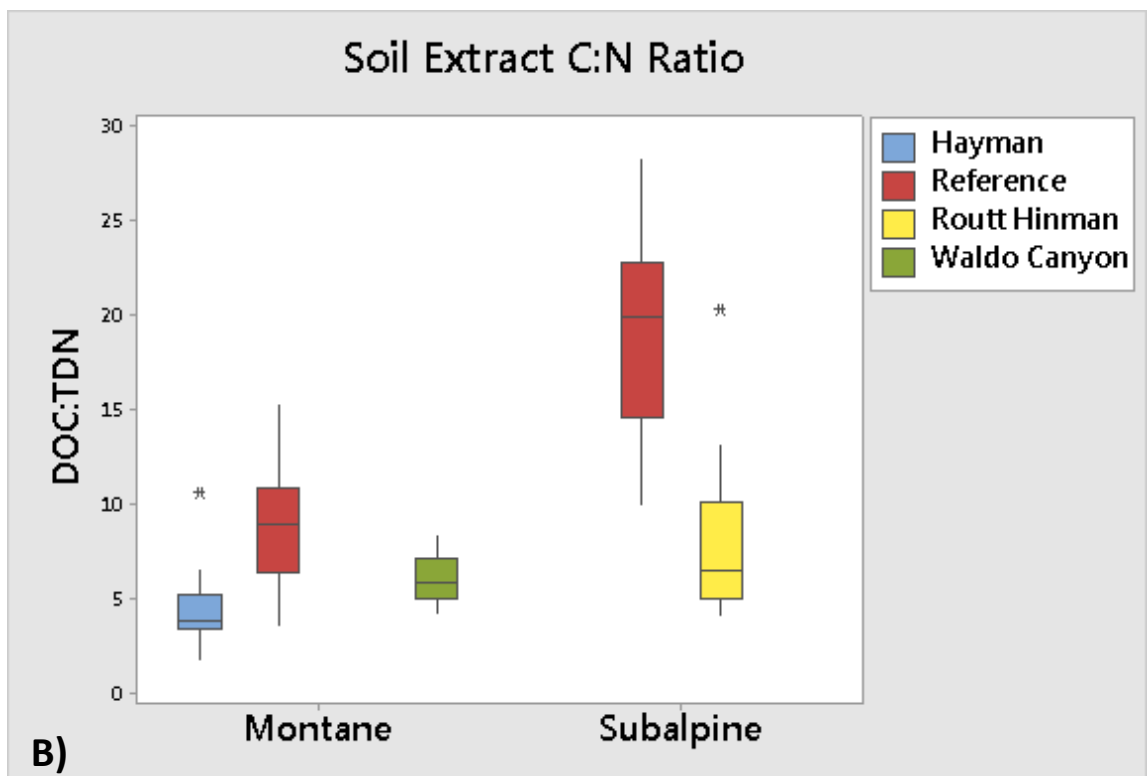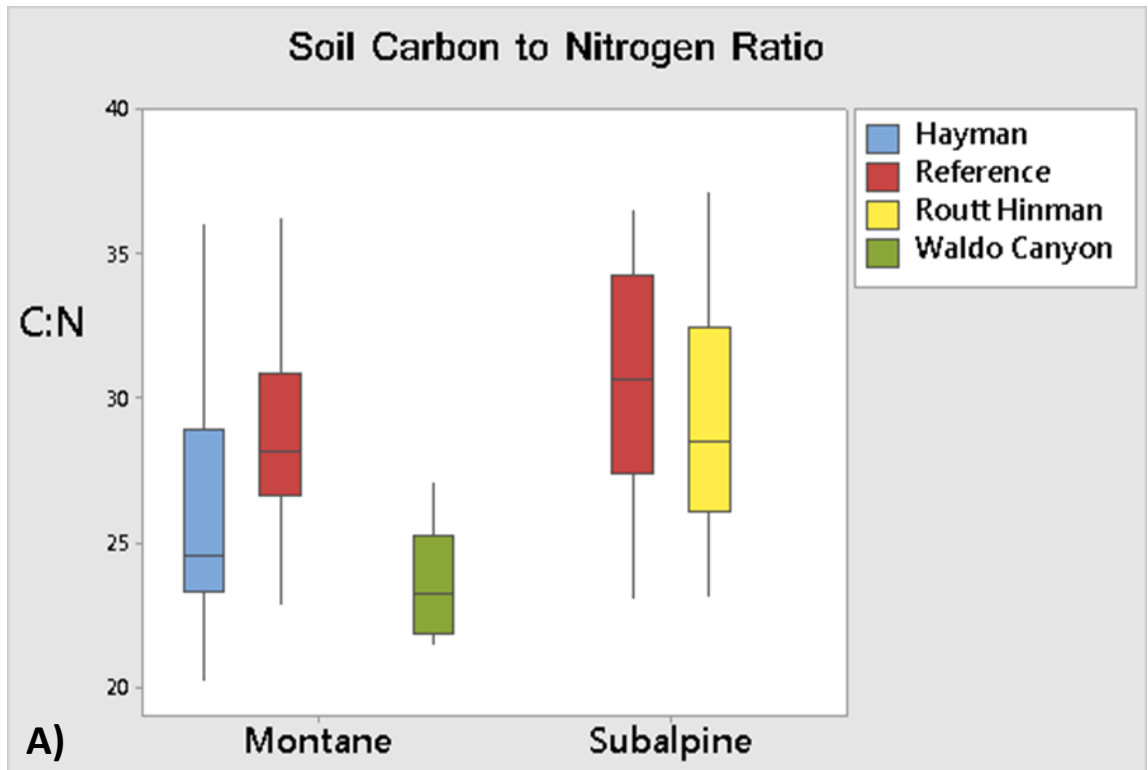
Figure 6. Concentrations of dissolved organic and inorganic nitrogen (including NH_4^+, NO_2^-, NO_3^-) in soil extracts. Sample sizes: HF n=18; HR n=14; RR n=18; RF n=19; WC n=6. Significant differences: Inorganic N: HR>RR ($p<0.1$); Organic N: RR>HR ($p<0.05$), RR>RF ($p<0.1$).
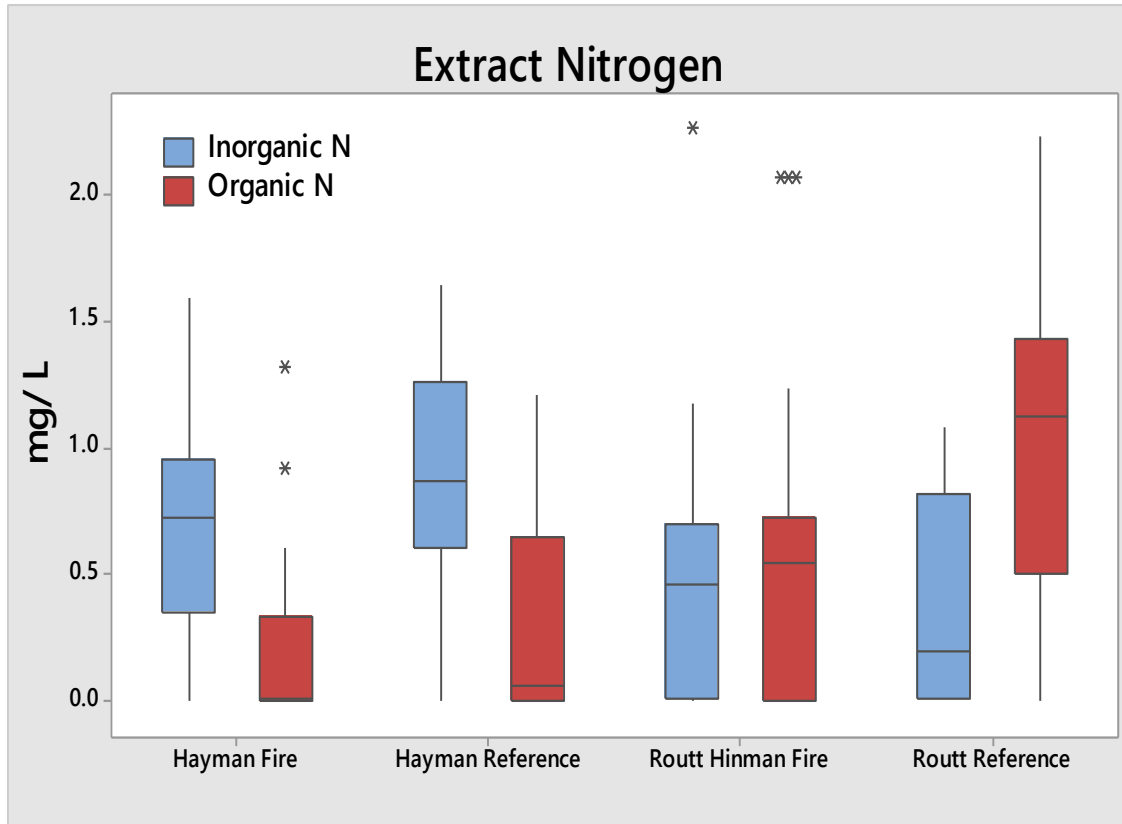
Figure 7. Proxy for soil C bioavailability over 11-week study period in Front Range watersheds and Routt Hinman area plots. Error bars represent one standard deviation from the mean. Each data point represents the mean respiration measurement for all soils in each watershed: Fourmile n=9; Pine n=9; Painted Rocks n=14, Dry n=6; Routt/Hinman n=19; Routt reference n=18.
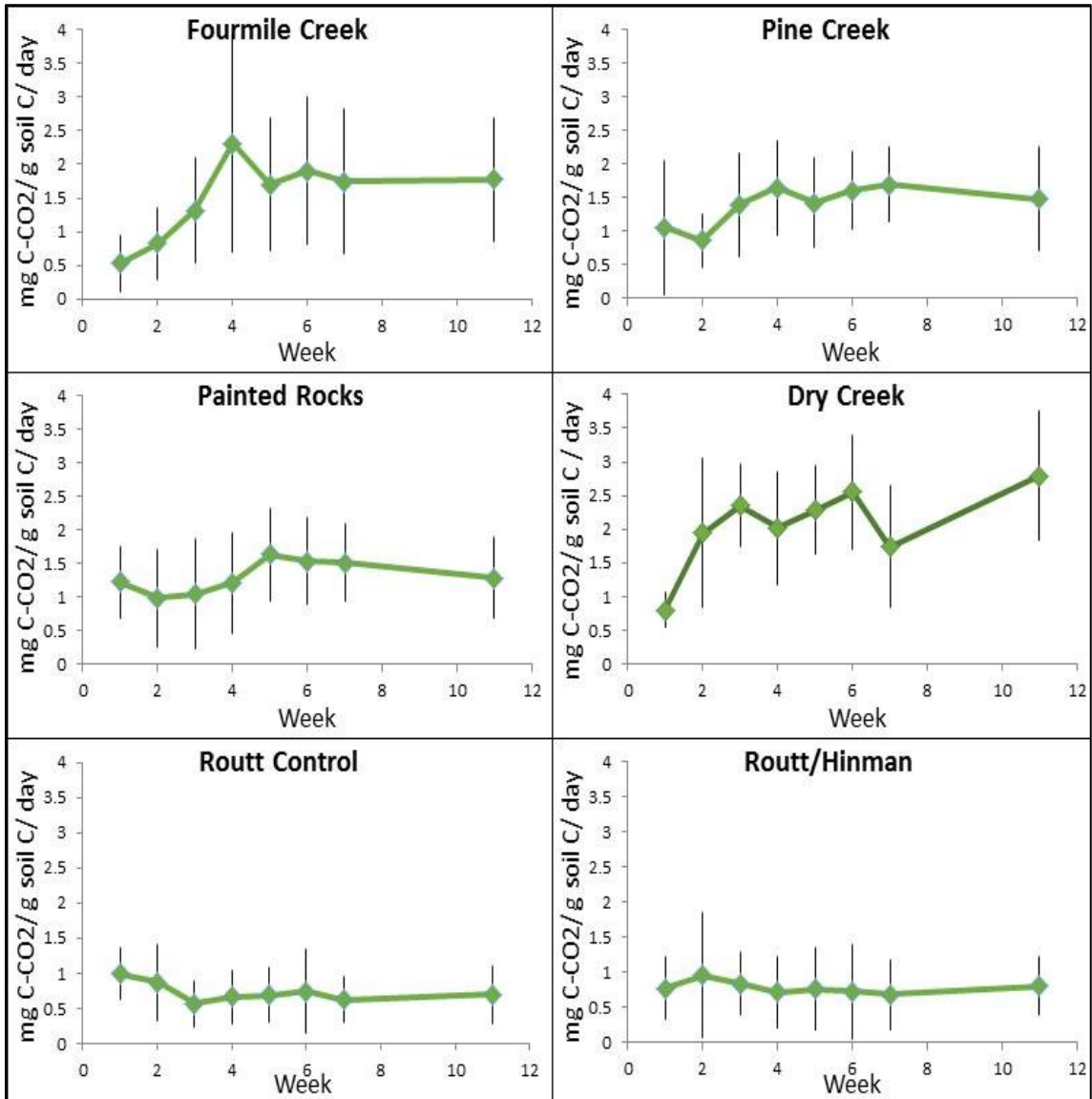
Figure 8. A) Soil respiration (mg C-CO$_2$) summed over 7 weeks, compared across ecosystem type and fire history. Significant differences: RR>RF, RR>HR, WC>HF. **B)** Proxy for soil C bioavailability (mg C-CO$_2$ g^{-1} soil C) summed over seven weeks, compared across ecosystem type and fire history. Significant differences: HF>HR. Sample sizes: HF n=18; HR n=14; RR n=18; RH n=19; WC n=6.
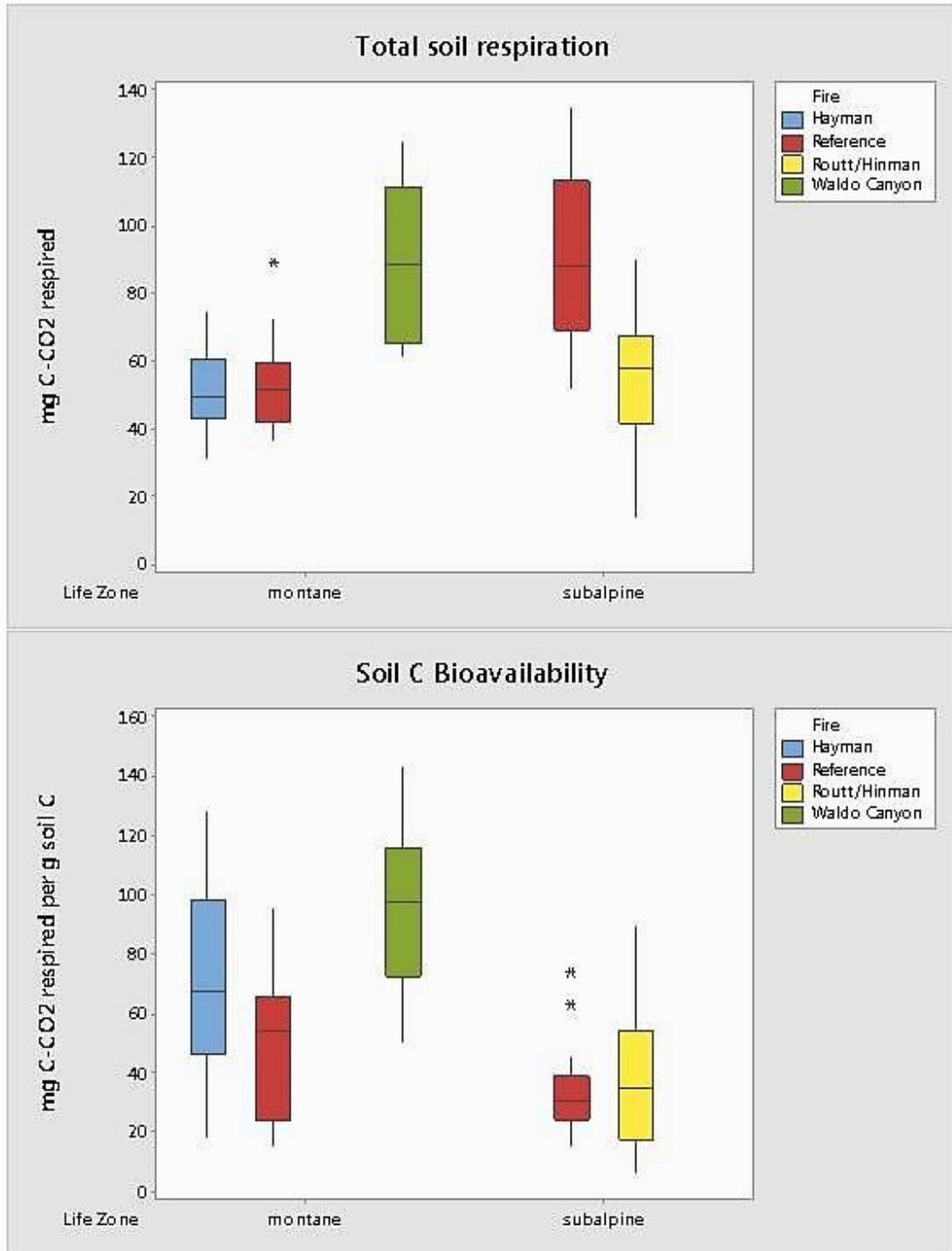
Figure 9. Proxy for soil C bioavailability (n=75) correlated with **A)** fine fraction soil % C; **B)** fine fraction soil %N; **C)** fine fraction soil C:N ratio; **D)** C:N of soil extract. All regressions are significant (p<0.05). Two outliers were removed (n=73).
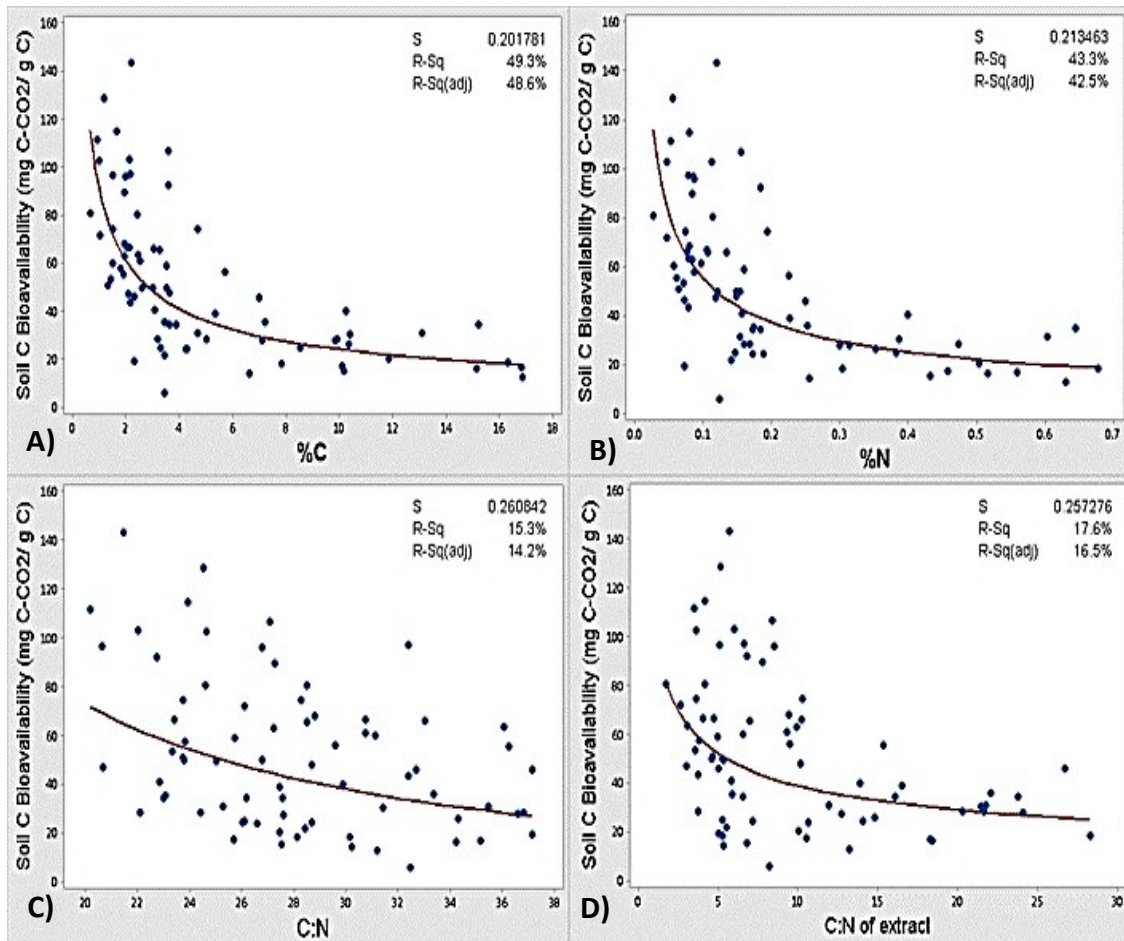
Figure 10. Soil C bioavailability (mg C-CO_2 g^{-1} soil C) correlated with: **A)** Soil % moisture (power relationship); **B)** Bulk density (g cm^{-3}); **C)** Aboveground biomass (Mg C ha^{-1}); **D)** Total soil C (Mg C ha^{-1}) (power relationship); **E)** BC on CWD (Mg C ha^{-1}). Though BC on CWD is 0 in all reference plots, there is still a positive correlation with soil C bioavailability within burn plots. **F)** Bioavailability correlated with total ecosystem C (Mg ha^{-1}), showing difference between ecosystems. Bioavailability is more C-dependent in the montane forest than in the subalpine forest. This ecosystem difference likely also accounts for the nonlinear relationship with total soil C and soil moisture; soil moisture is significantly different between forest types, and is correlated with total ecosystem C ($p<0.05$).
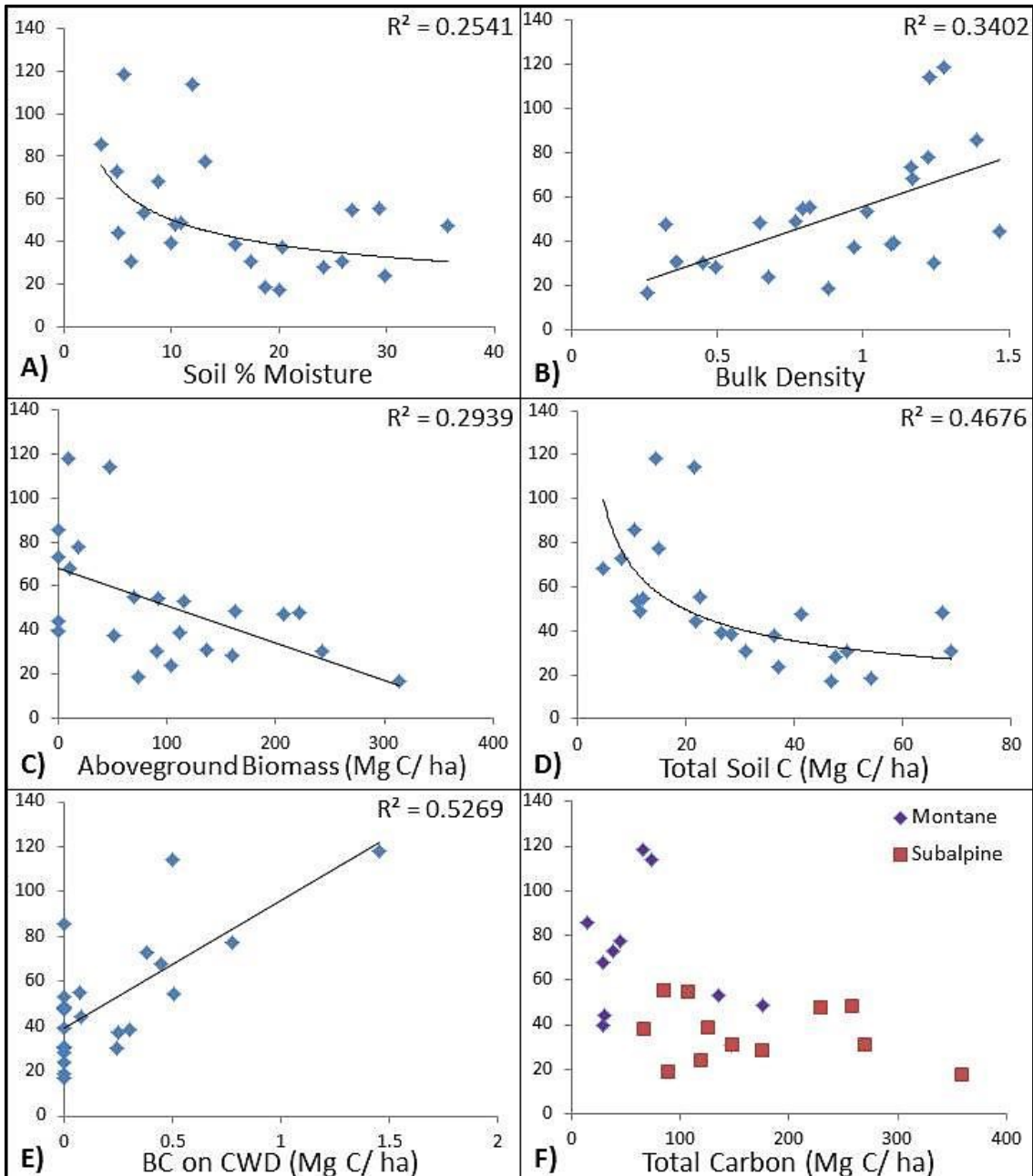
Figure 11. Fraction of precipitation exported to streams, calculated for each watershed from weekly stream discharge measurements over 9 weeks in June and July 2015; Sample sizes: Hayman n=23; Hayman reference n=8; Waldo Canyon n=21; Waldo Canyon reference n=9.
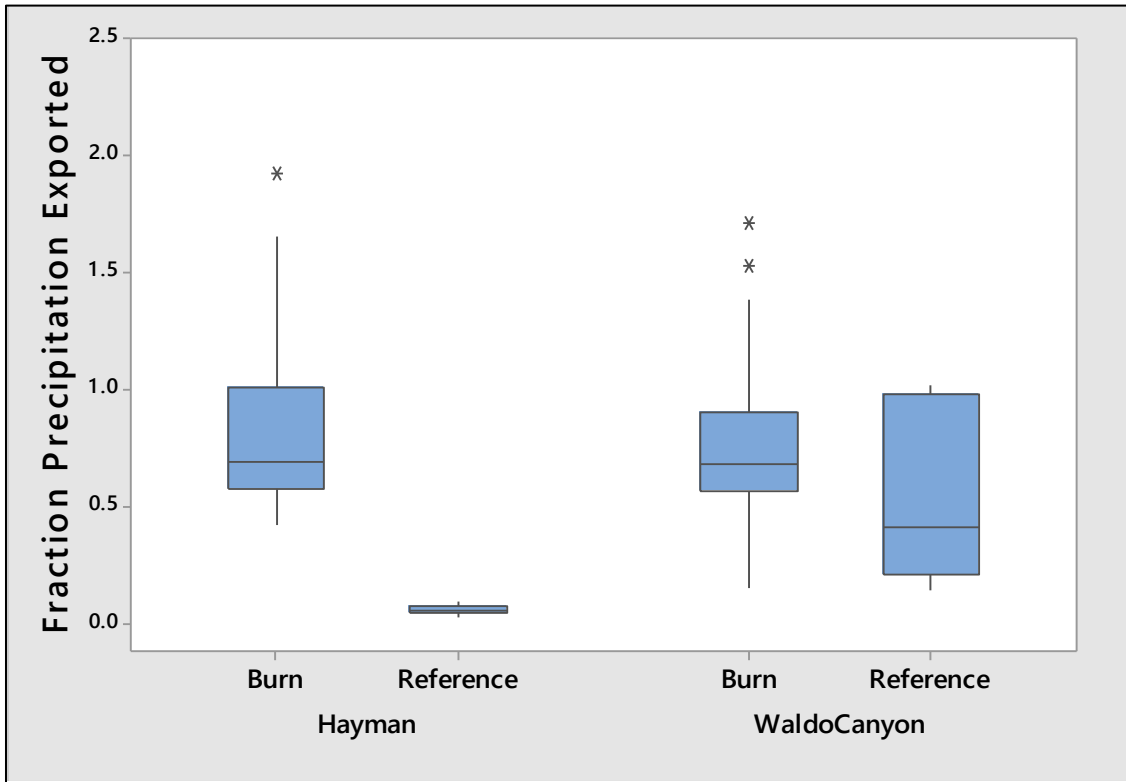
Figure 12. Carbon **(A)** and nitrogen **(B)** yield in g m^{-2} yr^{-1}, calculated from weekly discharge measurements and stream sample data for Front Range watersheds. **(C)** and **(D)** show DOC and TDN concentrations in mg L^{-1} from stream sample data. Arrows denote significant differences (p<0.05).
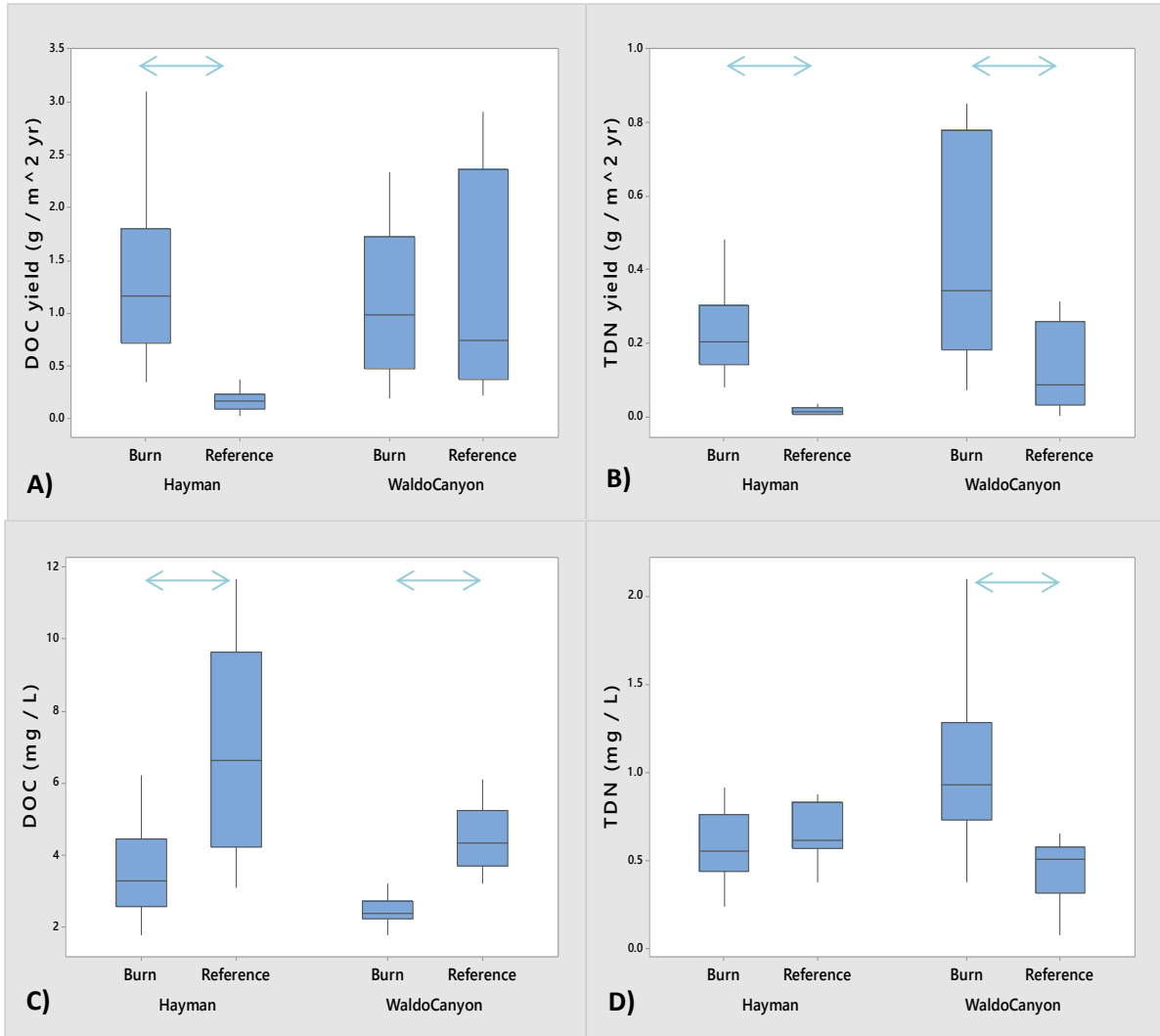
Figure13. Stream carbon **(A)** and nitrogen **(B)** concentrations and stream C:N ratio **(C)** graphed against spatial data for burn severity and extent, calculated in GIS for each of the Front Range watersheds. Fraction burned is the best predictor for DOC concentration (r= -0.658, p<0.001) and DOC:TDN ratio (r= -0.581, p<0.001). TDN concentration is best correlated with burn extent combined with low to moderate severity burn (r=0.722, p<0.001). Bars show 95% confidence interval for the mean.

A)

Individual standard deviations are used to calculate the intervals.

B)

Individual standard deviations are used to calculate the intervals.

C)

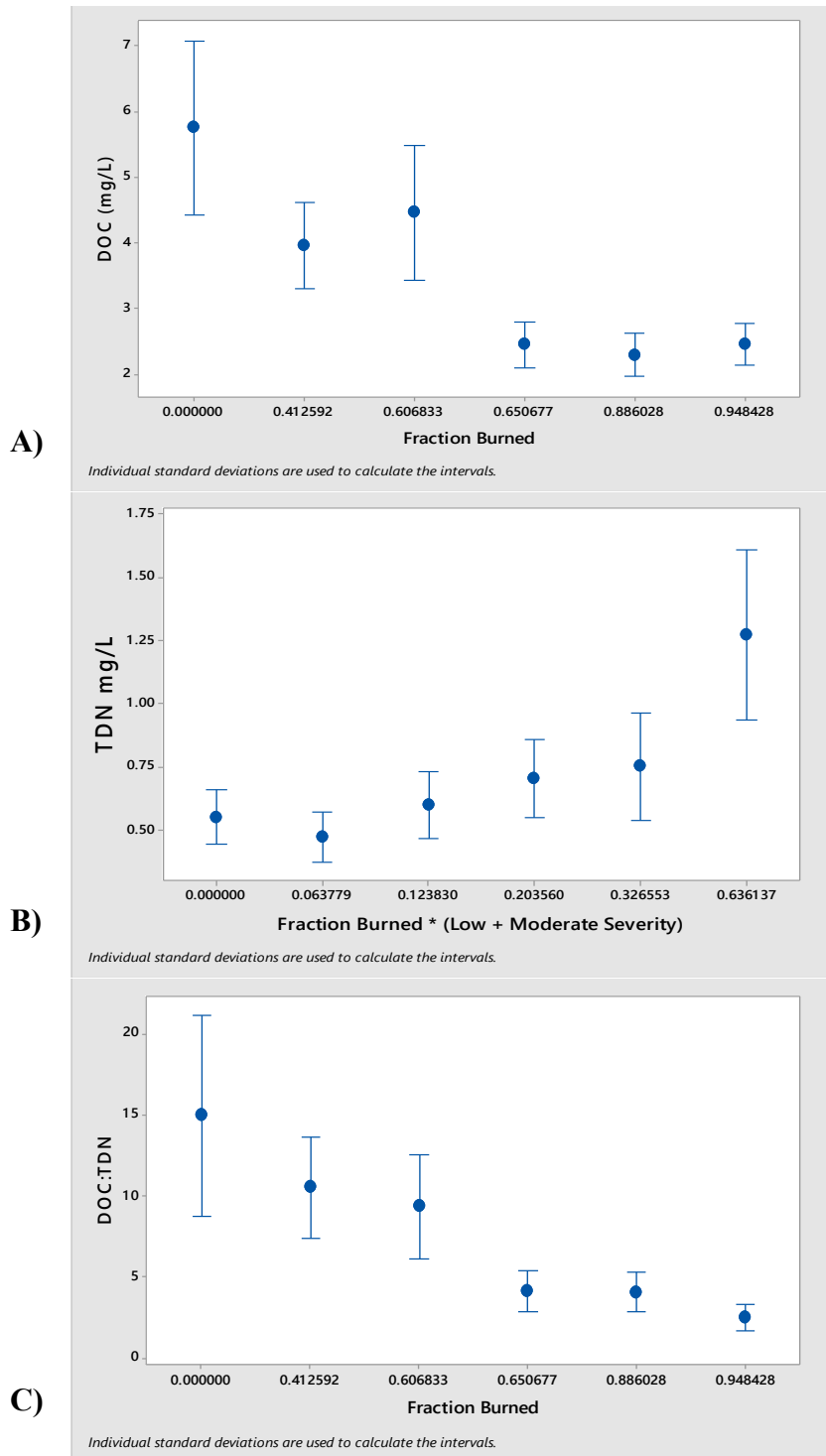*Individual standard deviations are used to calculate the intervals.*

Figure 14. Diagram of factors affecting soil microbial activity. Includes both direct determinants of the rate of microbial activity (C quantity and quality, oxygen, soil moisture, and temperature, and microbial community composition) and indirect determinants (size and composition of vegetative community, soil nutrients, soil organic matter, soil physical properties), all of which are affected by fire. General information on determinants of microbial activity came from Chapin 2011.
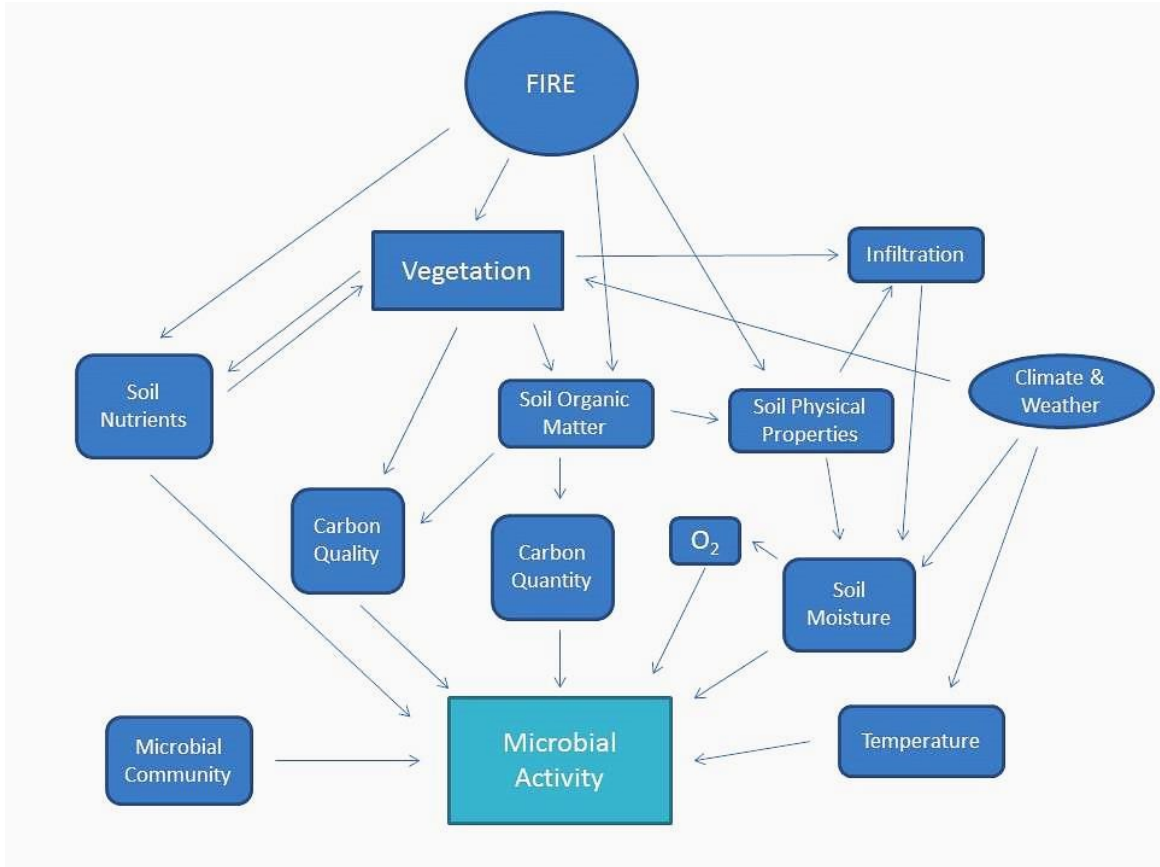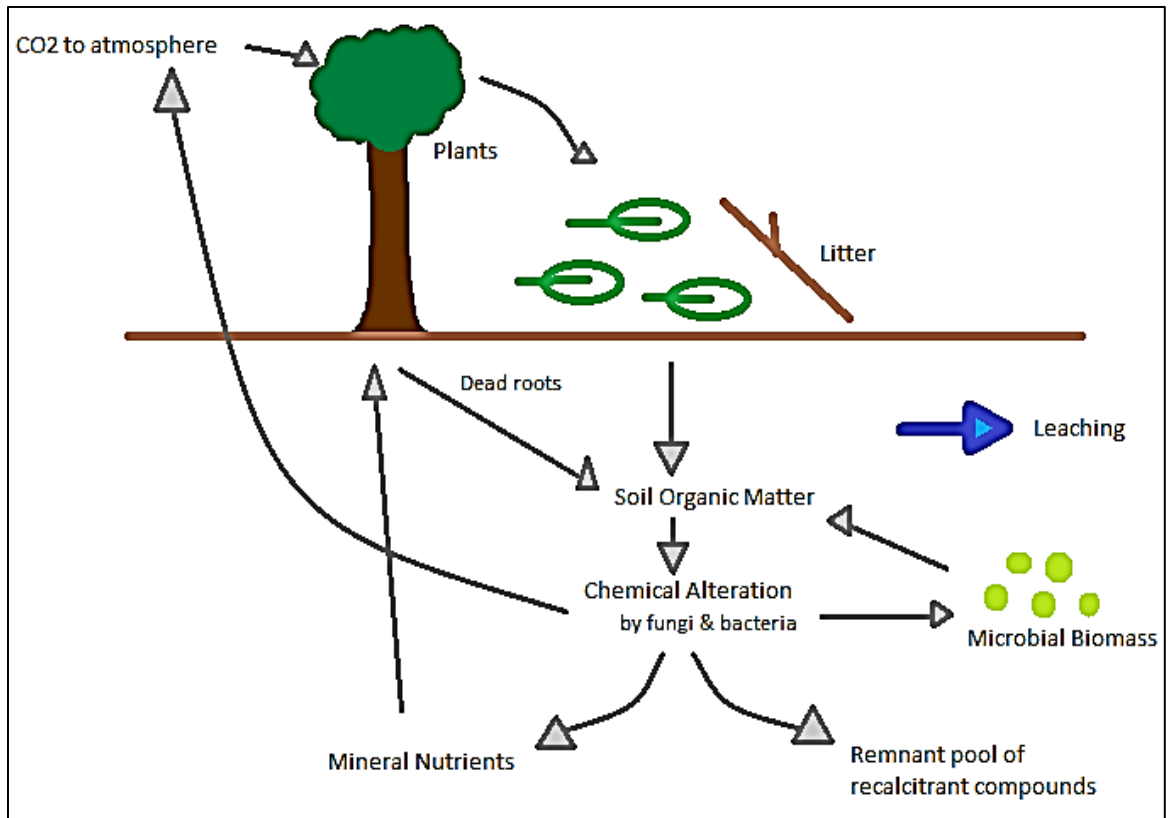
Figure 15. Diagram of soil C inputs and exports. General information from Chapin 2011.

9. APPENDICES

Appendix I.

Precision, range of standard concentrations, and range of sample concentrations of ions measured using the Dionex ICS-5000. Precision calculated as the average standard deviation between replicate measurements, excluding replicates which fell outside of the range of detection. For NO_2^-, Br^-, and Li^+, precision could not be calculated because none of the replicated samples had high enough concentrations of those ions to be detected. While the range of standards is large, some of the more concentrated standards were excluded from the calibration curves because the samples themselves were very dilute. Minimum sample concentrations for all ions fell below the detection limit, and were not reported here.

	F^-	Cl^-	NO_2^-	SO_4^{2-}	Br^-	NO_3^-	PO_4^{3-}	Li^+	Na^+	NH_4^+	K^+	Mg^{2+}	Ca^{2+}
Precision ± ppm	0.086	0.027	0	0.602	0	0.143	0.268	0	0.012	0.0002	0.107	0.0533	0.267
Std. Min. (ppm)	0.04	0.06	0.20	0.30	0.20	0.20	0.30	0.07	0.27	0.003	0.27	0.27	1.37
Std. Max. (ppm)	10.0	14.9	50.0	74.5	49.5	49.5	74.0	12.5	50.2	100.7	50.2	50.0	251.5
Sample Max. (ppm)	1.43	3.91	0.55 / 5	3.58	0.567	5.25	2.15	0	5.13	1.11	4.31	2.33	20.7

Appendix II. Pearson's correlations for all variables. Values highlighted in yellow are significant (p<0.05). Values highlighted in green have p<0.10.

Terrestrial Analysis

SOIL DATA: Variables with measurements for individual soil samples (n=3 per plot). DOC, TDN, and ion concentrations are from soil extracts. %C, %N, and soil C:N are for fine fraction soil:

	Bioavailability (mg C-CO_2 g^{-1} soil C)	%C	%N	Soil C:N
%C	−0.546			
%N	−0.532	0.981		
Soil C:N	−0.400	0.278	0.129	
DOC mg L^{-1}	−0.360	0.657	0.666	0.209
TDN mg L^{-1}	−0.257	0.352	0.367	0.146
C:N of extract	−0.439	0.650	0.626	0.359
Chloride	0.166	−0.063	−0.062	−0.092
Sulfate	−0.001	0.052	0.069	−0.033
Nitrate	0.199	−0.301	−0.293	−0.108
Phosphate	−0.067	−0.070	−0.069	0.026
Sodium	−0.057	−0.048	−0.056	0.163
Ammonium	−0.053	0.204	0.241	−0.064
Potassium	−0.116	0.263	0.281	0.054
Magnesium	0.190	0.078	0.102	−0.104
Calcium	0.200	0.168	0.197	−0.134

PLOT DATA: Variables with estimates for each plot, correlated with bioavailability proxy. BC refers to black carbon.

	Bioavailability
Total Soil C Mg ha^{-1}	-0.609
Aboveground C Mg ha^{-1}	-0.569
Aboveground char Mg ha^{-1}	0.632
Coarse soil % char	-0.428
Coarse soil % roots	-0.436
BC on CWD Mg ha^{-1}	0.726
CWD Mg C ha^{-1}	-0.125
Grass Mg C ha^{-1}	-0.418
Forb Mg C ha^{-1}	0.169
Total Mg C ha^{-1}	-0.483
Soil Bulk Density	0.583
Soil Moisture %	-0.429

FRONT RANGE PLOTS: Variables with values only for Front Range terrestrial plots (Hayman and Waldo Canyon fires). Percent variables refer to percent of ground cover from field measurements:

	Bioavailability
%vegetation	-0.330
%dirt	0.732
%litter	-0.533
Shrub Mg C ha^{-1}	0.516

Watershed Analysis

STREAM DATA: Data from discharge and stream chemistry measurements in Hayman and Waldo Canyon watersheds during June/July 2015. Precipitation from PRISM climate dataset. Burn extent & severity data from MTBS dataset. Severity variables refer to the fraction of the watershed burned with low, moderate, and high severity fire. For DOC and TDN, both concentration (mg L^{-1}) and yield (g m^{-2} yr^{-2}) are included:

	DOC mg L^{-1}	TDN mg L^{-1}	SUVA	DOC:TDN
TDN mg L^{-1}	-0.272			
SUVA	0.244	-0.253		
DOC:TDN	0.546	-0.577	0.132	
Q m^{3} yr^{-1}	-0.001	-0.303	0.386	0.086
Precipitation	-0.296	0.729	-0.341	-0.494
% precip exported	-0.278	0.077	-0.189	-0.227
DOCyield	-0.092	-0.017	0.022	-0.125
TDNyield	-0.304	0.362	-0.299	-0.326
Fraction Burned	-0.658	0.509	-0.282	-0.581
Low Severity	-0.539	0.651	-0.581	-0.498
Moderate Severity	-0.613	0.634	-0.426	-0.562
High Severity	-0.347	-0.012	0.190	-0.279
Slope	-0.406	-0.194	-0.203	-0.140
Frtn*HiSeverity	-0.382	0.073	0.080	-0.312
Frtn*Lo+Modsever	-0.547	0.722	-0.501	-0.518

	DOCyield	TDNyield
TDNyield	0.794	
Fraction Burned	0.071	0.322
Low Severity	0.117	0.462
Moderate Severity	0.114	0.409
High Severity	-0.032	-0.030
Slope	0.495	0.406
% precip exported	0.919	0.923