**Multi-decadal impacts of high-severity wildfire on ecosystem nitrogen cycling**

Allison E. Rhea1, Charles C. Rhoades2, and Timothy P. Covino1

1Colorado State University, Department of Ecosystem Science and Sustainability

2 US Forest Service Rocky Mountain Research Station, Fort Collins, CO

# **1 Introduction**

Fire can have profound impacts on the amount, form, and distribution of nitrogen (N) in soils, groundwater and streams (Certini, 2005; Wan et al., 2001). Substantial N stocks are lost from the combustion of the O horizon and occasionally upper mineral soils during high severity fire (Bormann et al., 2008; Johnson et al., 2005). The pyrolysis of organic matter initiates an immediate pulse of ammonium (NH4+) from soils to streams (Covington & Sackett, 1992; Grogan et al., 2000; Raison, 1979; Wan et al., 2001). Nitrification is then stimulated by increased NH4+ concentrations (Hanan et al., 2016), favorable abiotic conditions (i.e., soil temperature, moisture, and pH) (Bauhus et al., 1993; Hanan et al., 2016), and the presence of char and ash (Bauhus et al., 1993; DeLuca & Sala, 2006) which causes a delayed, but more prolonged pulse of nitrate (NO3-) (Covington & Sackett, 1992; Wan et al., 2001). Mineral N that is not taken up by plants or microbes is often leached from soils in the mobile, dissolved form, NO3- (Gresswell, 1999; Turner et al., 2007) or eroded and deposited downslope as N-rich soil or ash (Grogan et al., 2000; Lane et al., 2008; Pierson et al., 2019).

Recent work suggeststhat fire impacts on ecosystem N cycling can last longer than was previously acknowledged*.* For example, stream NO3- and total dissolved N have remained elevated for 14 years following the 2002 Hayman Fire in Colorado (Rhoades et al., 2019). This indicates a significant and sustained reduction in ecosystem N retention (Rhoades et al., 2019) which could result from larger soil N pools (Certini, 2005; Turner et al., 2007), higher net N transformations (Dove et al., 2020; Kurth et al., 2014), lower plant demand (Hart et al., 2005), or some combination therein. While these mechanisms have been well documented immediately post-fire (< 5 years, Covington & Sackett, 1992; Grogan et al., 2000; Raison, 1979; Wan et al., 2001), there is a need for long-term studies to investigate the potential drivers of elevated inorganic N decades after fire.

It is generally accepted that vegetation should begin exerting a greater influence over N cycling than soil microbes during post-fire regeneration through root exudation, plant litter inputs, increased nutrient uptake, and formation of symbioses with soil microorganisms (Hart et al., 2005; Kaye & Hart, 1997; Vitousek & Reiners, 1975) though the increasing size and severity of wildfires may challenge these assumptions (Dove et al., 2020). For example, ponderosa pine (*Pinus ponderosa*) and Douglas-fir (*Pseudotsuga menziesii*) rely on live trees as seed sources (Bonnet et al., 2005) so post-fire regeneration has been slow after fires with large, high severity patches(Chambers et al., 2016; Rother & Veblen, 2016). This can cause burned forests to remain in grass- or shrub-dominated states for extended periods (Roccaforte et al., 2012) which is becoming more common (Coop et al., 2020; Tepley et al., 2017; Walker et al., 2018) as fire severity increases (Parks & Abatzoglou, 2020) and greater annual moisture deficits limit seedling recruitment (Stevens-Rumann et al., 2018). Slow forest recovery of large, high severity burn patches may ultimately sustain post-fire inorganic N export by limiting vegetation N uptake compared to unburned forests (Kurth et al., 2014).

The goals of this study were to 1) assess whether N pools and net transformation rates were still elevated in burned mineral soils decades after fire and 2) identify the underlying mechanisms sustaining elevated post-fire N concentrations in streams. To do so,we measured inorganic N concentrations, leaching, and mineralization in unburned watersheds dominated by ponderosa pine and burned watersheds that lack forest vegetation cover 17 years after the Hayman fire. Because soil, vegetation, fire behavior, and post-fire recovery all vary along topographic gradients (Hinckley et al., 2017; Holyman et al., 2018; Malone et al., 2018; Rother & Veblen, 2016), we distributed our burn and unburn comparisons of N cycling from uplands to streamside riparian zones. Given the history of elevated stream NO3- after the Hayman fire (Rhoades et al., 2011, 2019), we hypothesized that soil inorganic N pools and net transformation rates would be higher and vegetation demand would be lower in burned compared to unburned sites.

# **2 Methods**

## **2.1 Site Description**

The 2002 Hayman Fire burned 550 km2 of Colorado’s Pike National Forest (Figure 1a) which is dominated by ponderosa pine (*Pinus ponderosa*) and Douglas-fir (*Pseudotsuga menziesii*) (Graham, 2003). The understory plant community is dominated by grasses (*Bromus* spp. and *Poa* spp.), wood’s rose (*Rosa woodsii*), American red raspberry (*Rubus idaeus*), and *Geranium* sp. The majority of the Hayman Fire and our study area is underlain by the Pike’s Peak batholith (Ruleman et al., 2011), which is comprised of medium to coarse-grained biotite and hornblende-biotite granite and weathers to form weakly developed coarse, sandy loam soils (i.e., Ustorthents and Cryorthents) (Moore, 1992; Robichaud et al., 2013). Coarse fragments comprised 29% of the soil volume on average. Mean clay, silt, and sand fractions are 18, 23, and 59%. The depth of mineral soil ranges from 0-40 cm (Moore, 1992). The top 5 cm of mineral soils had a mean bulk density of 1.6 g/cm3 and pH ranged from 6.54 to 7.33. This semi-arid region receives an annual average of 40 cm of precipitation (WRCC, 2021) from both snow and summer monsoons and falls within the intermittent snow zone meaning snow cover does not persist throughout the winter (Richer et al., 2013).

This study compared inorganic N in soils, groundwater and streams burned by the 2002 Hayman fire with those from unburned landscapes. All sampling occurred 16-18 years post-fire. A vast majority of the sampling occurring in the summer of 2019 though initial soil samples were collected for analysis of baseline physical and chemical properties (i.e. soil texture, bulk density, pH, and C and N content) in the summer of 2018 and winter ion exchange resins were deployed from October 2019 until May of 2020. This study included 16 hillslope gradients (i.e., 8 burned, 8 unburned) that spanned near-stream riparian positions, toeslopes at the concave slope break, and midslope positions on the lower hillslope (Figure 1). We established a plot at each topographic position that included 3 field replicates. We also sampled 20 upland plots (10 burned and 10 unburned) that were further upslope on low-gradient hillslopes (Figure 1). Uplands were sampled with a different sampling design that was not constrained by proximity to a stream and did not include plot-level field replicates (Figure 1). We used a physical definition of the various topographic positions based on elevation above stream to calculate the spatial extent of each – riparian <2 m above stream, toe and midslope 2-8 m above stream, and uplands >8 m above stream. Riparian position comprised 2-4% of the study watersheds, toe and midslopes 4-7%, and uplands 89-95%.

## **2.2 Vegetation sampling**

We used the point-intercept method in 1 m2 quadrats to characterize surface cover at each plot. Vegetation was differentiated into forb, graminoid, and shrub classes and surface cover was classified as follows: organic horizon, mineral soil, rock, moss/lichen, char, coarse wood (> 7.5 cm), fine wood (< 7.5 cm), coarse roots (> 0.5 cm), fine roots (< 0.5 cm) and other (e.g., scat, bone). We also extracted a remotely-sensed estimate of annual terrestrial net primary productivity (NPP, kg C/m2) for our study area in 2018. Because this product is constrained to a 30-m resolution, we report one value for each riparian, toeslope, and midslope sequence and one value for each upland plot. Foliar N pools increase with aboveground NPP (Turner et al., 2009), so we use annual NPP as a proxy for vegetation N demand.

## **2.3 Soil Sampling**

In the summer of 2018, three mineral soil cores (0-15 cm) were collected from each topographic position and sieved to 2 mm to remove coarse fragments. The O horizon (i.e., forest floor) was also sampled in unburned upland positions. A 20 g sub-sample from mineral and organic horizons was dried at 105°C for 24 hours, ground in a roller table for 72 hours, and analyzed for total soil C and N content (%) by Dumas dry combustion (LECO CHN 2000; St Joseph, MI). pH was measured for mineral soils in a 1:1 supernatant of 10 g sub-sample of mineral soil and a slurry of DI. C and N stocks of mineral and O horizons were then calculated by multiplying bulk density by soil depth and % C and N content. We assumed O horizon bulk densities of 0.14 g/cm3 (Stephens et al., 2004) and upland mineral soil bulk densities of 1.39 g/cm3 (Robichaud et al., 2013).

In June of 2019, three mineral soil cores (0-15 cm) were again collected from each topographic position to measure extractable inorganic N pools and net production rates. All soils were sieved to 2 mm and an initial 20 g subsample was extracted with 100 mL of 2M KCl, shaken for 60 minutes, filtered, and analyzed for NO3- and NH4+ using spectroscopy (Lachat QuikChem AutoAnalyzer FIA+ 800 Series, Loveland, CO). A second 10 g subsample was oven dried at 105°C for 24 hours to calculate gravimetric moisture content (GMC). A 50 g sub-sample was placed in a loosely capped plastic cup in a 20°C aerobic incubation chamber for 14 days (Binkley & Hart, 1989). Samples were rewetted with DI water periodically to maintain field moisture content. After 14 days, subsamples of the incubated soils were extracted and analyzed as described above. Net mineralization was calculated as the difference in NO3- plus NH4+ in the initial and incubated soils, net nitrification as the change in NO3-, and ammonification as the change in NH4+ (Hart et al., 1994).

We used ion exchange resins (IER) as a measure of soil inorganic N availability (NO3- and NH4+) for plant uptake and soil infiltration by adsorbing N in soil solution to the resin surface. Soil N availability was measured using a 1:1 mixture of cation and anion exchange resin beads (Binkley & Matson, 1983). Six IER bags were buried at 5 cm depth in the mineral soil at each topographic position (i.e., 2 IER bags at each of the 3 plot replicates). We included two deployment periods – May 2019 to October 2019 and October 2019 to May 2020 which were respectively defined as summer and winter deployments. At the end of the incubation period, removed resins were extracted with 100 mL of 2M KCl, shaken for 60 minutes, filtered, and frozen until they were analyzed for NO3- and NH4+ concentrations as described above.

We measured volumetric moisture content (VMC) monthly from June to September of 2019 using a handheld time domain reflectometry instrument with a 20 cm probe (CD 620, HydroSense Campbell Scientific, Logan UT). Three to four measurements were recorded at each plot replicate and VMC was averaged by plot.

## **2.4 Water sampling**

We measured surface and shallow groundwater chemistry and water level in two burned (B1-2) and two unburned (U1-2) watersheds (Figure 1a). We instrumented each of these sites with a stream monitoring station, two riparian groundwater wells, two nested piezometers, and 14 tension lysimeters. The riparian wells were installed on both sides of the stream to a completion depth of 1 m to sample riparian groundwater. The nested piezometers were installed to depths of 40 cm and 80 cm in the center of the stream bed to sample hyporheic water. Porous cup, tension lysimeters (Soil Moisture Corp, Goleta, CA) were installed to a depth of 30 cm to sample soil water leachate with 6 in the riparian zone, 6 in toeslope positions, 3 in midslope positions, and none in the uplands given the dry soil conditions.

We sampled stream water 1-2 times per month (5/13, 5/28, 6/12, 6/24, 7/8, 7/22, 8/3, 8/20, 9/14). We sampled shallow groundwater from the riparian wells and nested piezometers on the same dates using a peristaltic pump that was purged with DI water and a sample rinse prior to each sample collection. Soil water leachate was sampled throughout the summer (5/14, 5/29, 6/25, 7/17, 8/7, 9/15) using a hand pump following the same procedures. All water samples were stored on ice in acid-washed HDPE plastic bottles and filtered through 0.45 µm filters (Millipore Durapore PVDF, Billerica, MA). NO3- and NH4+ concentrations were measured with ion chromatography (Dionex Corp., Sunnyvale, CA). Detection limits were 0.01 mg/L for both and concentrations that fell below detection limits were replaced by one half the detection limit concentration (0.005 mg/L). This was only common for lysimeter samples were sample volumes were so low, were required to run dilutions.

TruTrack capacitance rods (Intech Instruments Ltd. New Zealand) were installed in all streams, wells, and piezometers to record stage every 15 minutes from May to October of 2019. These data were averaged by day to reduce noise and converted to station-specific z scores to allow for comparisons between stations. Manual water level measurements were also recorded biweekly throughout the summer field season to check continuously recorded water levels.

## **2.5 Statistical analysis**

All measured variables were screened for outliers and averaged at the plot level. Subsequent analyses were conducted on the plot means. T-tests were used to determine whether measured soil, vegetation, and water properties varied with burn condition while stratifying by topographic position. ANOVA was used to determine if these parameters varied with topographic position while stratifying by burn condition All statistical analyses were conducted in R (R Development Core Team) and significance was determined at the α = 0.05 level.

# **3 Results**

## **3.1 Seasonal moisture dynamics**

Over the course of the 2019 water year, the Cheesman weather station recorded 16.7 cm of rainfall (WRCC, 2021). The Glen Cove SNOTEL station recorded 37.4 cm of snow water equivalent (NRCS, 2021), but was located south of Hayman, near Pikes Peak at 3,500 m so the magnitude of snowfall was likely lower at our study sites where mean elevation was 2,500 m. Most snowfall occurred in March though snow storms continued through May and most rainfall peaked in July (Figure 2). The South Platte stream gauge (USGS, 2021) demonstrated peak flows in late June during snowmelt though there were multiple rainfall-driven peaks throughout the season (Figure 2). Our study watersheds were much smaller (i.e., first order streams draining into the South Platte) and exhibited similar, but muted seasonal trends in streamflow (Supplemental Figure 1). The volumetric moisture content in the top 20 cm of mineral soils declined throughout the summer sampling period and moving from riparian to upland positions, but was generally similar in burned and unburned soils (Supplemental Figure 2).

## **3.2 Vegetation cover**

Substrate cover only varied significantly with burn condition in upland positions where O horizon cover was lower and mineral soil and char cover were higher in burned compared to unburned plots (Figure 3a). In burned plots, O horizon decreased and mineral soil cover increased with distance from stream (Figure 3a). Substrate cover did not vary much with landscape position in unburned plots. Forb and graminoid cover were generally higher in burned plots though statistical significance varied with topographic position (Figure 3b). Shrub cover was variable, but was significantly higher in burned uplands than unburned uplands (Figure 3b).

Mean annual NPP was 5,666 and 4,669 kg C/m2 in unburned riparian corridors and uplands and 1,750 and 1,351 kg C/m2 in burned riparian corridors and uplands. Thus, unburned forests had three-times greater vegetation N demand compared to shrub-dominated, burned plots (Figure 3b). Unburned uplands were dominated by ponderosa pine and Douglas Fir though aspen were also found in the toeslopes. No burned plots had live conifers though half of the burned toeslope plots had some aspen regeneration.

## **3.3 Soil C and N stocks**

Mean C content ranged from 1.6% to 33% and was an order of magnitude higher in O horizon samples compared to mineral soils (Table 1). The total C content of unburned mineral soils was generally greater than, though not significantly different from, burned soils. Mean C stocks in the top 5 cm of mineral soils were 2,027 g C/m2 in unburned plots and 1,914 g C/m2 in burned plots which represents an average post-fire loss of 6%. Mineral soil C stocks were the highest in toeslope positions and lowest in upland positions (Table 1). Total C was 1,620 g C/m2 lower in burned than unburned uplands when summed across the top 5 cm of mineral soils (108 g C/m2 lost) and the O horizon (1,512 g C/m2 lost) which is similar to previously reported losses of 1,900 g C/m2 (Bormann 2008).

Mean N content ranged from 0.07% to 0.87% and was generally similar in burned and unburned mineral soils (Table 1). N stocks were 102 g N/m2 in top 5 cm of unburned mineral soils and 105 g N/m2 in burned mineral soils, representing a 3% increase. Mineral soil N stocks were also the highest in toeslope positions and lowest in upland positions (Table 1). Mineral soil total N was reduced by 45 g N/m2 in burned uplands when summed across the top 5 cm of mineral soils (10 g N/m2 increase) and O horizon (55 g N/m2 loss) which again is similar to previously reported losses of 55 g N/m2 (Bormann 2008).

## **3.4 Mineral soil inorganic N**

Mean soil extractable NO3- concentrations were 1.75 mg/kg in burned mineral soils and 0.64 mg/kg in unburned mineral soils (Figure 4a). While NO3- concentrations did not vary significantly with burn condition, there was on average 4-times more NO3- in burned midslopes than unburned midslopes (Figure 4a, p=0.06). Within burned sites, midslopes had the highest and uplands the lowest NO3- concentrations whereas NO3- did not vary with topographic position in unburned sites (Figure 4a). Mean soil extractable NH4+ concentration did not vary significantly with burn condition or topographic position (Figure 4b). NO3- comprised 51% of DIN on average in burned soils and 34% in unburned soils.

Over the winter, resin-sorbed NO3- was 2.4-times greater in burned midslopes compared to unburned midslopes (Figure 5a). Winter resin-sorbed NO3- was also 2.8-times greater than summer resin-sorbed NO3- in burned midslopes. Resin-sorbed NO3- did not vary with burn condition in any other topographic position or over the summer deployment period (Figure 5a). Resin-sorbed NH4+ was higher in burned than unburned soils, with the exception of uplands (Figure 5b).

## **3.5 Inorganic N production in mineral soils**

Net ammonification rates were negative or near zero across all landscape positions and burn conditions (Figure 6). In contrast, net nitrification and mineralization rates were positive in all unburned soils and burned uplands (Figure 6). Burned soils in lower topographic positions (i.e., riparian, toeslope, and midslope) exhibited negative or near zero nitrification and mineralization rates (Figure 6). Given the high observed variability, neither ammonification, nitrification, nor N mineralization varied significantly with burn condition though nitrification rates were marginally lower in burned midslopes compared to unburned midslopes (p=0.08).

## **3.6 Water N Concentrations**

Both stream and shallow groundwater had higher NO3- concentrations in burned compared to unburned watersheds whereas soil water NO3- was much lower in both burned and unburned watersheds (Figure 7). Mean soil water NO3- was 0.21 mg/L in burned soils and 0.14 mg/L in unburned soils which is lower than NO3- concentrations observed in other water bodies (Figure 7a). Shallow groundwater NO3- concentrations from the riparian wells and nested piezometers were also consistently higher in burned (0.64-4.07 mg/L) compared to unburned watersheds (0.01-3.42 mg/L) (Figure 7b-c). Stream NO3- concentrations were consistently higher in burned (0.67-4.25 mg/L) compared to unburned watersheds (0.01-0.59 mg/L) (Figure 7d). NH4+ concentrations only ranged from 0.005 mg/L (i.e. detection limit) to 0.75 mg/L across all sampling locations and dates. On average NH4+ comprised 7% of DIN in unburned water samples and 1% of DIN in burned water samples.

# **4 Discussion**

Most ecosystems have substantial capacity to store added nitrogen in soils and vegetation (Chapin et al., 2005). However, there is evidence that severe wildfire reduces the capacity of forested watersheds to retain atmospheric N inputs. It was estimated that 97% of pre-fire N inputs to forested headwater catchments were retained within vegetation and soils, but that value declined to <50% after severe wildfire (Rhoades et al., 2019). We hypothesized that this post-fire loss of N retention capacity could be the product of larger soil N pools (Certini, 2005; Turner et al., 2007), higher net N transformations (Dove et al., 2020; Kurth et al., 2014), lower plant demand (Hart et al., 2005), or some combination therein. We investigate these potential drivers to improve our understanding long-term ecosystem resilience to severe wildfires that are becoming more frequent in the 21st century.

## **4.1 Evaluating changes in soil N pools and net transformation**

Ecosystem C and N stocks control terrestrial productivity (Chapin et al., 2011) and can be substantially reduced by high severity fire (Bormann et al., 2008). There was evidence of large C and N losses from O horizon combustion (~1,500 g/m2 and 50 g/m2 of C and N respectively) and erosion (7-225 g/m2 and 0.3-11 g/m2 of C and N over 4 post-fire years) (Pierson et al., 2019) after the Hayman fire. However C and N stocks remained relatively similar in burned and unburned mineral soils (Table 1) because mineral soils have a higher heat capacity than O horizons, making them less susceptible to combustion losses (Neary et al., 1999).Mineral soil C stocks were only reduced by 6%, on average, which is similar to the 11% reductions reported in a meta-analysis of 57 fires (Nave et al., 2011). Conversely, we saw a 5% increase in mineral soil N stocks post-fire. While this finding differs from previously reported 12% reductions (Nave et al., 2011), it is not entirely surprising. Combustion losses of N from severe fire are generally small relative to total pre-fire stocks (Page-Dumroese & Jurgensen, 2006) and soil N retention can increase after fire due to the incorporation of N into microbial biomass (Xu et al., 2022).

The slight changes in mineral C and N stocks lowered C:N ratios in burned mineral soils (19:1) compared to unburned mineral soils (23:1), though these differences were not statistically significant. Because nitrogen mineralization rates tend to increase with decreasing substrate C:N ratios (Chapin et al., 2011), we might expect mineralization to be higher in burned mineral soils. However, both burned and unburned mineral soils fell below the critical threshold (C:N of 25:1) that microbes require to meet their nitrogen requirements (Chapin et al., 2011) suggesting that soil microbes would be C-limited, rather than N-limited, in both burned and unburned soils. Net N mineralization rates were similar in burned and unburned mineral soils (Figure 6) in the absence of underlying differences in substrate quality.

Observed nitrification rates, and consequently soil NO3- concentrations, were also similar in burned and unburned soils (Figures 4 and 6). While fire can stimulate nitrification (DeLuca & Sala, 2006; Kurth et al., 2014) through increased NH4+ (Hanan et al., 2016) and favorable abiotic conditions (i.e., soil temp, moisture, and pH) (Bauhus et al., 1993; Hanan et al., 2016), and the presence of char and ash (Bauhus et al., 1993; DeLuca & Sala, 2006), these stimulatory effects are generally short-term (Covington & Sackett, 1992; Grogan et al., 2000; Raison, 1979; Wan et al., 2001). For example, our observed soil NH4+ concentrations were much lower than other values reported immediately post-fire (<33 mg/L, Turner et al., 2007) and were similar in burned and unburned mineral soils (Figure 4). Similarly, nitrification rates did not vary with pH because pH was similar in burned and unburned soils. However, N transformation rates have been shown to decrease with time since fire in mineral soils, but increase with time in O horizons (Yermakov & Rothstein, 2006) so there may be unmeasured increases in O horizon mineralization in our burned plots.

Overall, we found similar total C and N stocks, inorganic N concentrations, and N transformations rates (i.e., N mineralization and nitrification) in burned and unburned mineral soils. Together, these results demonstrate that there are no lasting changes to soil inorganic N supply 17 years after severe wildfire, corroborating numerous other studies that demonstrate short-term soil responses (Covington & Sackett, 1992; Grogan et al., 2000; Raison, 1979; Wan et al., 2001).

## **4.2 Evidence of persistent plant-mediated NO3- losses**

Following fire, mineral N that is not taken up by plants or microbes is either eroded and deposited downslope as N-rich soil or ash (Grogan et al., 2000; Lane et al., 2008; Pierson et al., 2019) or leached through soils to hillslope groundwater in the mobile, dissolved form, NO3- (Gresswell, 1999; Turner et al., 2007). While particle-associated fractions dominate N exports immediately post-fire (Lane et al., 2008), these contributions decline sharply within 2 years post-fire due to reduced sediment delivery (Pierson et al., 2019). However dissolved NO3- tends to have a slower recovery, likely due to elevated nitrification or persistent leaching (Lane et al., 2008, Rhoades et al., 2019). Indeed, stream NO3- concentrations were 10-times higher in burned compared to unburned watersheds (Figure 7). This pattern has been consistent throughout 15 years of post-fire monitoring and across flow states (Rhoades et al., 2011, 2019). However, N transformation rates were similar in burned and unburned mineral soils (Figure 6) so instead, we propose that elevated post-fire stream NO3- is sustained by reduced vegetation demand and the leaching of excess NO3- into hillslope groundwater.

To characterize the production and transport of NO3- throughout these watersheds, we explored the relationship between NO3- concentration and streamflow over time (Arora et al., 2020; Creed et al., 2015; Godsey et al., 2009). In the two unburned watersheds, stream NO3- concentrations decreased linearly with increasing stream stage (Figure 8). This dilution behavior is associated with the depletion of a finite resource (i.e., NO3-) within a catchment or the mixing with dilute waters (i.e., source-limited) (Basu et al., 2011; Godsey et al., 2009) and has been observed in watersheds with strong terrestrial N limitation where high rates of vegetation uptake and microbial assimilation limit the transport of inorganic N (Shogren et al., 2021). Undisturbed conifer forests are generally strongly N-limited (Schlesinger & Bernhardt, 2013) and these unburned watersheds have high vegetation N demands (Figure 3b) which would constraint the potential for NO3- export. In contrast, the two burned watersheds exhibited chemostatic behavior where stream NO3- varied little in response to increasing stream stage (Figure 8). This chemostatic behavior can be caused by the storage and release of legacy solutes that buffer variation in biogeochemical processing (Basu et al., 2011). In the context of this study, we propose that this shift from source-limitation in unburned watersheds to chemostatic behavior in burned watershed is driven by the build-up of N in the shallow groundwater of burned watersheds. Our data demonstrate that groundwater NO3- concentration are significantly higher in burned compared to unburned watersheds (Figure 7) and are negatively related to terrestrial NPP (Figure 9). Even though N supply is similar in burned and unburned watersheds, vegetation N demand is three-times lower in burned compared to unburned watersheds. Thus, nutrient supply from atmospheric deposition, N-fixation, and organic matter decomposition remains higher than plant demand in burned watersheds, stimulating NO3- losses to groundwater.

It has been suggested that water quality problems in receiving waters will persist until the legacy stores are substantially depleted (Basu et al., 2010). Within the context of this study, post-fire legacy stores appear to be driven by reduced vegetation demand so regeneration would have to occur at the landscape-scale in order to mitigate NO3- losses to groundwater. However, post-fire regeneration has been slow, particularly in dry conifer forests (Chambers et al., 2016; Rother & Veblen, 2016; Stevens-Rumann et al., 2018). This is driven in part by increasing climate water deficits that have created unfavorable post-fire growing conditions and increased regeneration failures in the 21st century (Coop et al., 2020; Stevens-Rumann et al., 2018). Furthermore, large, severe wildfires can limit post-fire recruitment by extending the distance to seed sources beyond a viable range (~50 m) (Chambers et al., 2016; Rother & Veblen, 2016). As a result, large high severity patches have exhibited little to no ponderosa pine regeneration, even 10 years post-fire (Chambers et al., 2016; Rother & Veblen, 2016) and this trend of poor regeneration is only expected to worsen as the occurrence of high severity fire increases across the Western US (Parks & Abatzoglou, 2020).

Research conducted after the mountain pine beetle outbreak may offer a useful example of a targeted mitigation approach. After insect infestation killed 50-60% of the trees in a forested watershed, significant NO3- losses accumulated in soil water and hillslope groundwater (Biederman et al., 2016). However, N removal in riparian zones and streams significantly reduced exports such that only 13-16% of hillslope losses were measured in streams (Biederman et al., 2016). Our previous work at the Hayman fire demonstrated elevated in-stream N demand in burned watersheds 15 years post-fire, but terrestrial N supply still greatly exceeded in-stream demand (Rhea et al., 2021). This demonstrates the limited capacity for stream retention and highlights riparian zones as strategic locations to target for post-fire restoration. We concur with previous work that called for targeted tree planting in exposed headwater riparian zones (Rhoades et al., 2019) and suggest also considering restoration strategies that enhance hydrologic connection, variable redox conditions, and slow residence times to maximize nitrate reductions (McClain 2003, Vidon and Hill 2004). As large, severe disturbances become more common, targeted restoration will be a critical tool to increase watershed N retention capacity.

# **5. Conclusions**

Stream N exports have remained elevated for decades after the Hayman fire indicating that post-fire impacts on ecosystem N cycling may persist longer than we previously acknowledged. The goal of this research was to characterize the long-term persistence of elevated soil nutrient pools and turnover and investigate the mechanistic drivers of these trends. We hypothesized that soil inorganic N pools and net transformation rates would be higher and vegetation demand would be lower in burned compared to unburned sites. However, total C and N, inorganic N concentrations, and N transformation rates were similar in burned and unburned mineral soils. Therefore, persistent N losses are not driven by a change in soil inorganic N supply 17 years post-fire. Rather, this post-fire response appears to be the consequence of reduced vegetation N demand leading to the accumulation of groundwater NO3- in burned watersheds which will continue exporting NO3- to streams until vegetation N demand increases substantially.

# **References**

Arora, B., Burrus, M., Newcomer, M., Steefel, C. I., Carroll, R. W. H., Dwivedi, D., et al. (2020). Differential C-Q Analysis: A New Approach to Inferring Lateral Transport and Hydrologic Transients Within Multiple Reaches of a Mountainous Headwater Catchment. *Frontiers in Water*, *2*(August), 1–20. https://doi.org/10.3389/frwa.2020.00024

Basu, N. B., Thompson, S. E., & Rao, P. S. C. (2011). Hydrologic and biogeochemical functioning of intensively managed catchments: A synthesis of top-down analyses. *Water Resources Research*, *47*(10), 1–12. https://doi.org/10.1029/2011WR010800

Bauhus, J., Khanna, P. K., & Raison, R. J. (1993). The effect of fire on carbon and nitrogen mineralization and nitrification in an australian forest soil. *Australian Journal of Soil Research*, *31*(5), 621–639. https://doi.org/10.1071/SR9930621

Biederman, J. A., Meixner, T., Harpold, A. A., Reed, D. E., Gutmann, E. D., Gaun, J. A., & Brooks, P. D. (2016). Riparian zones attenuate nitrogen loss following bark beetle-induced lodgepole pine mortality. *Journal of Geophysical Research G: Biogeosciences*, *121*(3), 933–948. https://doi.org/10.1002/2015JG003284

Binkley, D., & Hart, S. C. (1989). The Components of Nitrogen Availability Assessments in Forest Soils. In B. A. Stewart (Ed.), *Advances in Soil Science* (10th ed.). Springer-Verlag.

Binkley, D., & Matson, P. (1983). Ion Exchange Resin Bag Method for Assessing Forest Soil Nitrogen Availability. *Soil Science Society of America Journal*, *47*(5), 1050–1052. https://doi.org/10.2136/sssaj1983.03615995004700050045x

Bonnet, V. H., Schoettle, A. W., & Shepperd, W. D. (2005). Postfire environmental conditions influence the spatial pattern of regeneration for Pinus ponderosa. *Canadian Journal of Forest Research*, *35*(1), 37–47. https://doi.org/10.1139/x04-157

Bormann, B. T., Homann, P. S., Darbyshire, R. L., & Morrissette, B. A. (2008). Intense forest wildfire sharply reduces mineral soil C and N: The first direct evidence. *Canadian Journal of Forest Research*, *38*(11), 2771–2783. https://doi.org/10.1139/X08-136

Certini, G. (2005). Effects of fire on properties of forest soils: A review. *Oecologia*, *143*(1), 1–10. https://doi.org/10.1007/s00442-004-1788-8

Chambers, M. E., Fornwalt, P. J., Malone, S. L., & Battaglia, M. A. (2016). Patterns of conifer regeneration following high severity wildfire in ponderosa pine – dominated forests of the Colorado Front Range. *Forest Ecology and Management*, *378*, 57–67. https://doi.org/10.1016/j.foreco.2016.07.001

Chapin, F. S., Mooney, H. A., & Matson, P. A. (2011). *Principles of Terrestrial Ecosystem Ecology* (2nd ed.). New York, NY: Springer.

Coop, J. D., Parks, S. A., Stevens-Rumann, C. S., Crausbay, S. D., Higuera, P. E., Hurteau, M. D., et al. (2020). Wildfire-Driven Forest Conversion in Western North American Landscapes. *BioScience*, *70*(8), 659–673. https://doi.org/10.1093/biosci/biaa061

Covington, W. W., & Sackett, S. S. (1992). Soil mineral nitrogen changes following prescribed burning in ponderosa pine. *Forest Ecology and Management*, *54*(1–4), 175–191. https://doi.org/10.1016/0378-1127(92)90011-W

Creed, I. F., McKnight, D. M., Pellerin, B. A., Green, M. B., Bergamaschi, B. A., Aiken, G. R., et al. (2015). The river as a chemostat: Fresh perspectives on dissolved organic matter flowing down the river continuum. *Canadian Journal of Fisheries and Aquatic Sciences*, *72*(8), 1272–1285. https://doi.org/10.1139/cjfas-2014-0400

DeLuca, T. H., & Sala, A. (2006). Frequent fire alters nitrogen transformations in ponderosa pine stands of the Inland Northwest. *Ecology*, *87*(10), 2511–2522. https://doi.org/10.1890/0012-9658(2006)87[2511:FFANTI]2.0.CO;2

Dove, N. C., Safford, H. D., Bohlman, G. N., Estes, B. L., & Hart, S. C. (2020). High-severity wildfire leads to multi-decadal impacts on soil biogeochemistry in mixed-conifer forests. *Ecological Applications*, *0*(0), 1–18. https://doi.org/10.1002/eap.2072

Godsey, S. E., Kirchner, J. W., & Clow, D. W. (2009). Concentration–discharge relationships reflect chemostatic characteristics of US catchments. *Hydrological Processes*, *23*, 1844–1864.

Graham, R. T. (2003). *Hayman Fire Case Study*. *Gen. Tech. Rep. RMRS- GTR-114*. Ogden, UT. Retrieved from http://www.fs.fed.us/rm/hayman\_fire/

Gresswell, R. E. (1999). Fire and aquatic ecosystems in forested biomes of North America. *Transactions of the American Fisheries Society*, *128*(2), 193–221. https://doi.org/10.1577/1548-8659

Grogan, P., Bruns, T. D., & Chapin, F. S. (2000). Fire effects on ecosystem nitrogen cycling in a Californian bishop pine forest. *Oecologia*, *122*(4), 537–544. https://doi.org/10.1007/s004420050977

Hanan, E. J., Schimel, J. P., Dowdy, K., & D’Antonio, C. M. (2016). Effects of substrate supply, pH, and char on net nitrogen mineralization and nitrification along a wildfire-structured age gradient in chaparral. *Soil Biology and Biochemistry*, *95*, 87–99. https://doi.org/10.1016/j.soilbio.2015.12.017

Hart, S. C., Nason, G. E., Myrold, D. D., & Perry, D. A. (1994). Dynamics of gross nitrogen transformations in an old-growth forest: The carbon connection. *Ecology*, *75*(4), 880–891. https://doi.org/10.2307/1939413

Hart, Stephen C., DeLuca, T. H., Newman, G. S., MacKenzie, M. D., & Boyle, S. I. (2005). Post-fire vegetative dynamics as drivers of microbial community structure and function in forest soils. *Forest Ecology and Management*, *220*(1–3), 166–184. https://doi.org/10.1016/j.foreco.2005.08.012

Hinckley, E. L. S., Ebel, B. A., Barnes, R. T., Murphy, S. F., & Anderson, S. P. (2017). Critical zone properties control the fate of nitrogen during experimental rainfall in montane forests of the Colorado Front Range. *Biogeochemistry*, *132*(1–2), 213–231. https://doi.org/10.1007/s10533-017-0299-8

Holyman, Z. H., Jensco, K. G., Hu, J., Martin, J. T., Holden, Z. A., Seielstad, C. A., & Rowell, E. M. (2018). Hillslope Topograpy Mediates Spatial Patterns of Ecosystem Sensitivity to Climate. *Journal of Geophysical Research : Biogeosciences*, *123*, 353–371.

Johnson, D. W., Murphy, J. F., Susfalk, R. B., Caldwell, T. G., Miller, W. W., Walker, R. F., & Powers, R. F. (2005). The effects of wildfire, salvage logging, and post-fire N-fixation on the nutrient budgets of a Sierran forest. *Forest Ecology and Management*, *220*(1–3), 155–165. https://doi.org/10.1016/j.foreco.2005.08.011

Kaye, J. P., & Hart, S. C. (1997). Competition for nitrogen between plants and soil microorganisms. *Trends in Ecology & Evolution*, *12*(4), 139–143. https://doi.org/10.1126/science.158.3807.1426

Kurth, V. J., Hart, S. C., Ross, C. S., Kaye, J. P., & Fulé, P. Z. (2014). Stand-replacing wildfires increase nitrification for decades in southwestern ponderosa pine forests. *Oecologia*, *175*(1), 395–407. https://doi.org/10.1007/s00442-014-2906-x

Lane, P. N. J., Sheridan, G. J., Noske, P. J., & Sherwin, C. B. (2008). Phosphorus and nitrogen exports from SE Australian forests following wildfire. *Journal of Hydrology*, *361*(1–2), 186–198. https://doi.org/10.1016/j.jhydrol.2008.07.041

Malone, S. L., Fornwalt, P. J., Battaglia, M. A., Chambers, M. E., Iniguez, J. M., & Sieg, C. H. (2018). Mixed-severity fire fosters heterogeneous spatial patterns of conifer regeneration in a dry conifer forest. *Forests*, *9*(1). https://doi.org/10.3390/f9010045

Moore, R. (1992). Soil Survey of Pike National Forest, Eastern Park, Colorado. *USDA Forest Service and Soil Conservation Service*, 1–106.

Nave, L. E., Vance, E. D., Swanston, C. W., & Curtis, P. S. (2011). Fire effects on temperate forest soil C and N storage. *Ecological Applications*, *21*(4), 1189–1201. https://doi.org/10.1890/10-0660.1

NRCS. (2021). Daily Snow Water Equivalent Glen Cove, CO (Station 1057). Retrieved from https://wcc.sc.egov.usda.gov/nwcc/site?sitenum=1057

Page-Dumroese, D. S., & Jurgensen, M. F. (2006). Soil carbon and nitrogen pools in mid- to late-successional forest stands of the northwestern United States: Potential impact of fire. *Canadian Journal of Forest Research*, *36*(9), 2270–2284. https://doi.org/10.1139/X06-125

Parks, S. A., & Abatzoglou, J. T. (2020). Warmer and Drier Fire Seasons Contribute to Increases in Area Burned at High Severity in Western US Forests From 1985 to 2017. *Geophysical Research Letters*, *47*(22), 1–10. https://doi.org/10.1029/2020GL089858

Pierson, D. N., Robichaud, P. R., Rhoades, C. C., & Brown, R. E. (2019). Soil carbon and nitrogen eroded after severe wildfire and erosion mitigation treatments. *International Journal of Wildland Fire*, *28*(10), 814–821. https://doi.org/10.1071/WF18193

Raison, R. J. (1979). Modification of the soil environment by vegetation fires, with particular reference to nitrogen transformations: A review. *Plant and Soil*, *51*(1), 73–108. https://doi.org/10.1007/BF02205929

Rhoades, C. C., Entwistle, D., & Butler, D. (2011). The influence of wildfire extent and severity on streamwater chemistry, sediment and temperature following the Hayman Fire, Colorado. *International Journal of Wildland Fire*, *20*(3), 430–442. https://doi.org/10.1071/WF09086

Rhoades, C. C., Chow, A. T., Covino, T. P., Fegel, T. S., Pierson, D. N., & Rhea, A. E. (2019). The Legacy of a Severe Wildfire on Stream Nitrogen and Carbon in Headwater Catchments. *Ecosystems*, *22*(3), 643–657. https://doi.org/10.1007/s10021-018-0293-6

Richer, E. E., Kampf, S. K., Fassnacht, S. R., & Moore, C. C. (2013). Spatiotemporal index for analyzing controls on snow climatology: Application in the Colorado Front Range. *Physical Geography*, *34*(2), 85–107. https://doi.org/10.1080/02723646.2013.787578

Robichaud, P. R., Wagenbrenner, J. W., Lewis, S. A., Ashmun, L. E., Brown, R. E., & Wohlgemuth, P. M. (2013). Post-fire mulching for runoff and erosion mitigation Part II: Effectiveness in reducing runoff and sediment yields from small catchments. *Catena*, *105*, 93–111. https://doi.org/10.1016/j.catena.2012.11.016

Roccaforte, J. P., Fulé, P. Z., Chancellor, W. W., & Laughlin, D. C. (2012). Woody debris and tree regeneration dynamics following severe wildfires in arizona ponderosa pine forests. *Canadian Journal of Forest Research*, *42*(3), 593–604. https://doi.org/10.1139/X2012-010

Rother, M. T., & Veblen, T. T. (2016). Limited conifer regeneration following wildfires in dry ponderosa pine forests of the Colorado Front Range. *Ecosphere*, *7*(12). https://doi.org/10.1002/ecs2.1594

Ruleman, C. A., Bohannon, R. G., Bryant, Bruce, Shroba, R. R., & Premo, W. R. (2011). Geologic map of the Bailey 30’ x 60’ quadrangle, north-central Colorado: U.S. Geological Survey, Scientific Investigations Map SIM-3156, scale 1:100,000.

Schlesinger, W. H., & Bernhardt, E. S. (2013). *Biogeochemistry* (3rd ed.). Elsevier Inc. https://doi.org/https://doi.org/10.1016/C2010-0-66291-2

Shogren, A. J., Zarnetske, J. P., Abbott, B. W., Iannucci, F., Medvedeff, A., Cairns, S., et al. (2021). Arctic concentration–discharge relationships for dissolved organic carbon and nitrate vary with landscape and season. *Limnology and Oceanography*, *66*(S1), S197–S215. https://doi.org/10.1002/lno.11682

Stephens, S. L., Finney, M. A., & Schantz, H. (2004). Bulk density and fuel loads of ponderosa pine and white fir forest floors: Impacts of leaf morphology. *Northwest Science*, *78*(2), 93–100. Retrieved from https://www.researchgate.net/publication/289973466\_Bulk\_density\_and\_fuel\_loads\_of\_ponderosa\_pine\_and\_white\_fir\_forest\_floors\_Impacts\_of\_leaf\_morphology

Stevens-Rumann, C. S., Kemp, K. B., Higuera, P. E., Harvey, B. J., Rother, M. T., Donato, D. C., et al. (2018). Evidence for declining forest resilience to wildfires under climate change. *Ecology Letters*, *21*(2), 243–252. https://doi.org/10.1111/ele.12889

Tepley, A. J., Thompson, J. R., Epstein, H. E., & Anderson-Teixeira, K. J. (2017). Vulnerability to forest loss through altered postfire recovery dynamics in a warming climate in the Klamath Mountains. *Global Change Biology*, *23*(10), 4117–4132. https://doi.org/10.1111/gcb.13704

Turner, M. G., Smithwick, E. A. H., Metzger, K. L., Tinker, D. B., & Romme, W. H. (2007). Inorganic nitrogen availability after severe stand-replacing fire in the Greater Yellowstone ecosystem. *Proceedings of the National Academy of Sciences of the United States of America*, *104*(12), 4782–4789. https://doi.org/10.1073/pnas.0700180104

Turner, M. G., Smithwick, E. A. H., Tinker, D. B., & Romme, W. H. (2009). Variation in foliar nitrogen and aboveground net primary production in young postfire lodgepole pine. *Canadian Journal of Forest Research*, *39*(5), 1024–1035. https://doi.org/10.1139/X09-029

USGS. (n.d.). USGS 06700000 SOUTH PLATTE RIVER ABOVE CHEESMAN LAKE, CO. Retrieved from https://waterdata.usgs.gov/co/nwis/uv/?site\_no=06700000&PARAmeter\_cd=00065,00060

Vitousek, P. M., & Reiners, W. A. (1975). Ecosystem Succession and Nutrient Retention: A Hypothesis. *BioScience*, *25*(6), 376–381. https://doi.org/10.2307/1297148

Walker, R. B., Coop, J. D., Parks, S. A., & Trader, L. (2018). Fire regimes approaching historic norms reduce wildfire-facilitated conversion from forest to non-forest. *Ecosphere*, *9*(4). https://doi.org/10.1002/ecs2.2182

Wan, S., Hui, D., & Luo, Y. (2001). Fire effects on nitrogen pools and dynamics in terrestrial ecosystems: A meta-analysis. *Ecological Applications*, *11*(5), 1349–1365. https://doi.org/10.1890/1051-0761(2001)011[1349:FEONPA]2.0.CO;2

WRCC. (2021). Daily Total Precipitation Cheesman, Colorado (Station 053102). Retrieved from https://wrcc.dri.edu/cgi-bin/rawMAIN.pl?coCCHE

Xu, W., Elberling, B., & Ambus, P. L. (2022). Fire increases soil nitrogen retention and alters nitrogen uptake patterns among dominant shrub species in an Arctic dry heath tundra. *Science of the Total Environment*, *807*, 150990. https://doi.org/10.1016/j.scitotenv.2021.150990