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ORIGINAL ARTICLE

Reburning Before Recovery: Effects of Short-Interval Fire on Subalpine Forest Nitrogen Stocks and Fluxes

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Abstract

In forests adapted to infrequent (> 100-year) stand-replacing fires, novel short-interval (< 30-year) fires burn young forests before they recover from previous burns. Postfire tree regeneration is reduced, plant communities shift, soils are hotter and drier, but effects on biogeochemical cycling are unresolved. We asked how postfire nitrogen (N) stocks, N availability and N fixation varied in lodgepole pine (*Pinus contorta* var. *latifolia*) forests burned at long and short intervals in Grand Teton National Park (Wyoming, USA). In 2021 and 2022, we sampled 0.25-ha plots that burned as long-interval (> 130-year) stand-replacing fire in 2000 (n = 3) or 2016 (n = 3) and nearby plots of short-interval (16-year) fire that burned as stand-replacing fire in both years (n = 6 'reburns'). Five years postfire, aboveground N stocks were 31% lower in short- versus long-interval fire (77 vs. 109 kg N ha^{-1}, respectively) and 76% lower than 21-year-old stands that did not reburn (323 kg N ha^{-1}). However, soil total N averaged 1,072 kg N ha^{-1} and dominated ecosystem N stocks, which averaged 1,235 kg N ha^{-1} and did not vary among burn categories. Annual resin-sorbed nitrate was highest in reburns and positively correlated with understory species richness and biomass. *Lupinus argenteus* was sparse, and asymbiotic N fixation rates were modest in all plots (< 0.1 kg N ha^{-1} y^{-1}). Although ecosystem N stocks were unaffected, high-severity short-interval fire reduced and repartitioned aboveground N stocks and increased N availability. These shifts in N pools and fluxes suggest reburns can markedly alter N cycling in subalpine forests.

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Author Contributions MGT and CCC designed the study. MGT, REH, NGK, JAW and CCC performed the research. MGT, REH and NGK analyzed data. MGT wrote the manuscript with contributions from all coauthors.

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Graphical Abstract

Key words: biogeochemistry; disturbance ecology; fire regime; Greater Yellowstone; nutrient cycling.

Highlights

- Short-interval fire reduced aboveground N stocks, but ecosystem N was unaffected
- Annual resin-sorbed nitrate was highest in short-interval fire
- Cryptic N fixation rates were low and similar after short- and long-interval fire

Introduction

Understanding ecosystem effects of compound forest disturbances is of growing interest because disturbance legacies are reduced (Paine and others 1998; Johnstone and others 2016; Hughes and others 2019), and tree regeneration is often sparse (Brown and Johnstone 2011, 2012; Turner and others 2019a; Nolan and others 2021). In fire-adapted forests with historically long fire return intervals (FRI; > 100 years), the likelihood that young forests will burn before having recovered from previous fire (that is, 'short-interval fires' or 'reburns'; Prichard and others 2017, McColl-Gausden and others 2021) is rising as fire size, frequency and severity increase with climate change (Westerling 2016; Abatzoglou and Williams 2016; Kitzberger and others 2017; Parks and Abatzoglou 2020). Anomalous high-severity short-interval (< 30-year) fires are occurring in Australian eucalypt forests (Fairman and others 2017) and boreal (Brown and Johnstone 2011, 2012; Whitman and others 2019), lower montane (Donato and others 2016) and subalpine (Harvey and others 2016; Turner and others 2019a; Hoecker and Turner 2022) conifer forests of North America. Short-interval fires will likely become more common in the decades ahead, and there is a growing need to understand how they will shape postfire forest ecosystems.

Ecological effects of novel short-interval fires differ markedly from fires that burn within historical ranges of variability in forest ecosystems. Infrequent high-severity fires burn large mature trees, combusting live and dead fine fuels and converting live woody biomass to necromass, most of which remains in the ecosystem as standing dead

snags (for example, 98% of total prefire stem biomass; Wei and others 1997). Most (> 85%) prefire downed coarse wood also persists postfire (Tinker and Knight 2000; Johnson and others 2005; Donato and others 2016). Postfire tree regeneration arises from in situ and ex situ seed sources, and downed coarse wood accumulates over decades as fire-killed snags fall to the ground (for example, Nelson and others 2016; Kiel and others 2023a). In contrast, short-interval fires burn small young trees, often growing in dense stands with abundant live canopy fuels. The compact arrangement of canopy fuels and downed coarse wood supports greater fuel combustion (Brown and Johnstone 2011; Turner and others 2019a; Braziunas and others 2023). After a reburn, postfire tree regeneration is greatly reduced via immaturity risk (Keeley and others 1999); limited dispersal of propagules from surrounding short-statured young trees (Gill and others 2021, 2022); and hot dry microclimate (Hoecker and others 2020; Wolf and others 2021). Live and dead carbon (C) stocks are also substantially reduced (Brown and Johnstone 2011; Donato and others 2016; Pelligrini and others 2018; Turner and others 2019a; Fairman and others 2022), and C recovery can be delayed by decades (Turner and others 2019a). However, whether consequences of short-interval fire are similar for key nutrients, such as nitrogen (N), is not known.

Understanding effects of short-interval fires on N is important because northern conifer forests are typically N limited (Fahey and others 1985; Yang 1998; Kishchuk and others 2002; Elser and others 2007; LeBauer and Treseder, 2008; Högberg and others 2017). All fires initially reduce forest N stocks because N is oxidized as biomass combusts (Maynard and others 2014). In crown fires, N losses are driven by combustion of live tree foliage, fine fuels and litter (Page-Dumroese and Jurgensen 2006; Smithwick and others 2005; Johnson and Turner 2014). Fire effects typically do not extend into the mineral soil (Turner and others 1999; Smithwick and others 2009; Maynard and others 2014), and strong soil microbial sinks (Chapman and others 2006; Turner and others 2007) minimize additional postfire N losses (for example, via leaching; Minshall and others 1997; Romme and Turner 2004). Short-interval fires could cause ecosystem N stocks to ratchet down as live tree biomass and detrital pools decline (Chertov and others 2009; Perakis and others 2015; Figure 1) or nutrient partitioning ratios (soil N: plant N; Kranabetter and others 2016) change.

Short-interval fires could also alter plant-available N. Inorganic N is generally elevated after fire,

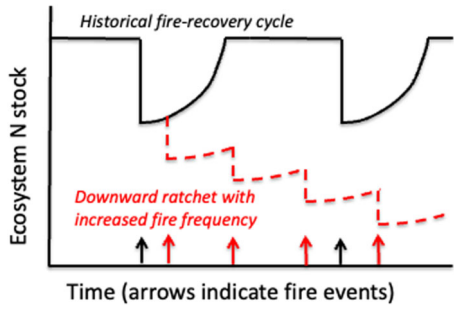

Figure 1. Hypothesized effects of repeated short-interval, high-severity fires that reburn aggrading forests before they recover from previous fire. We hypothesized such fires could trigger a 'ratchet' effect in which nutrient stocks decline over time. Black arrows indicate fires burning within their historical fire return interval (FRI), and red arrows indicate fires occurring at anomalously short FRI.

with an initial pulse of ammonium (NH_4^+) followed by a pulse of nitrate (NO_3^-), but these are usually ephemeral (for example, one or two years; Wan and others 2001; Hart and others 2005; Turner and others 2007; Smithwick and others 2009). Short-interval fires could have a persistent effect on available N if nitrification rates remained elevated because of a second pulse of charcoal (DeLuca and others 2006) or because pine needle litter, which depresses nitrification, is absent (Keeney 1980). Increased available N could enhance understory species richness and/or biomass because grasses and forbs are 'N-extravagant' plants that readily access mineralized N (Chapman and others 2006). Several species respond positively to fertilization (*Calamagrostis rubescens;* Romme and others 2009) or have higher foliar N concentrations following recent fire (*Arnica cordifolia, Carex geyeri, Vaccinium scoparium;* Metzger and others 2006).

With historically long FRI, ecosystem N stocks recover before forests burn again (Ryan and others 1997; Smithwick and others 2009; Dunnette and others 2014; Turner and others 2019b), and short-interval fires could affect N recovery if N inputs change. Nitrogen is replenished via biological N fixation (BNF; Vitousek and others 2013), and symbiotic N fixers have an advantage during early succession when light is plentiful (Johnson and others 2005; Sheffer and others 2015). However, N-fixing tree species are rare in many high-latitude forests (Menge and others 2016, 2017a, b, 2019), and how N capital is recovered after disturbance in N-poor forests with few symbiotic N fixers remains puzzling (Binkley and others 2000; Bormann and others 2002; Schoonmaker and others 2016; Menge and others 2017a, b; Tierney and others

2019; Turner and others 2019b). Where N-fixing trees are rare or absent, symbiotic fixation is typically associated with nodules of vascular shrubby or herbaceous plants (for example, Fabaceae, Rhamnaceae). Symbiotic N-fixing shrubs such as *Ceonothus velutinus* can dominate some postfire forests prior to canopy closure (Johnson and others 2012), and forbs such as *Lupinus argenteus* may be favored in reburns because of elevated light levels and reduced competition with trees (Schoennagel and others 2004; Romme and others 2016; Kiel and others 2023b). Asymbiotic or 'cryptic' sources of N fixation could also play a role (Wei and Kimmins 1998). Cryptic niches occur in soil, litter, lichens, moss, decomposing wood and mycorrhizae–rhizosphere bacteria (Reed and others 2011; Cleveland and others 2022), and a range of moss species recolonize wood, soil and rocks following fire (Eversman and Horton 2004).

We studied a natural experiment in which a 2016 stand-replacing fire reburned lodgepole pine forests that regenerated after a stand-replacing fire in 2000. Initial effects of this short-interval (16-year) fire included surprisingly high combustion of live and dead biomass, drastic reductions in postfire lodgepole pine regeneration and a projected additional 150 years for C stocks to recover (Turner and others 2019a). Effects on N stocks and fluxes could also be consequential, and here we asked, *How do short-interval (16-year) stand-replacing fires in a subalpine forest affect N stocks, N availability and N fixation?* and tested expectations for each of these responses (Table 1).

Methods

Study Area

We studied subalpine forests (ca. 2150 m elevation) in Grand Teton National Park (GRTE; Wyoming, USA) including areas where ecological responses to fire were assessed previously (Metzger and others 2006; Turner and others 2007; Romme and others 2009; Smithwick and others 2012; Turner and others 2019a; Hoecker and others 2020; Gill and others 2021). Lodgepole pine dominates GRTE between 2000 and 2400 m elevation, and stand-replacing fires have occurred at 100- to 300-year intervals throughout the Holocene (Loope and Gruell 1973; Whitlock 1993). The climate is continental, characterized by cold, snowy winters and mild, dry summers. Thirty-year (1991–2020) climate normals at the nearest weather station (YNP-Snake River Station; https://nowdata.rcc-acis.org/riw/ accessed 05/23/2024) report mean daily temperature and monthly precipitation of 14.1°C and 3.6 cm, respectively, for July, and − 10.4°C and 9.9 cm for January. Temperatures have risen by 1.3°C in Greater Yellowstone since 1950, and average temperatures between 2001 and 2020 were as high or higher than at any period in the last 20,000 years (Hostetler and others 2021). The parent material consists of Quaternary rhyolite bedrock and rhyolite-dominated glacial deposits, and soils are mostly Inceptisols (Typic Cryumbrepts and Dystric Chryocrepts). Atmospheric N deposition is low, averaging 1.67 kg N ha^{-1} y^{-1} (range 1.35–2.05) from 2011 to 2023 in GRTE (downloaded 05/20/2024 from https://nadp.slh.wisc.edu/networks/national-trends-network/ station WY94.)

Study Design

The study was conducted in areas burned by two fires (Figure 2). The 1,280-ha Glade Fire burned during summer 2000 in 120- and 150-year-old lodgepole pine forests that had regenerated after stand-replacing fires in 1856 and 1879, thus burning within the region's historical long FRI. The 8,500-ha Berry Fire burned during summer 2016 in similar old lodgepole pine forests and in 16-year-old lodgepole pines that regenerated after the Glade Fire (Figure 2). Thus, the Berry Fire included both historical long and novel short FRI. We selected study plots (n = 12) to contrast effects of short-interval fire with (a) areas burned as long-interval fire in the same most recent fire (2016) and (b) areas that regenerated after the same previous long-interval fire (2000) that had not reburned (Figure 2). Field research was highly constrained during summer 2021 because of the SARS-CoV-2 global pandemic, but we maximized our field effort given the restrictions that were in place. Nine plots were established initially in 2017 (Turner and others 2019a) and resampled for this study: six in areas of short-interval fire and three in areas of long-interval fire that regenerated after the 2000 Glade Fire (Figure 2). Three new plots were established in 2021 in nearby areas of long-interval fire that burned in 2016. All plots were 50 m × 50 m (0.25 ha) in size, oriented due north on areas with minimal slope and aspect, dominated by lodgepole pine before and after fire, and burned as stand-replacing fire (100% mortality of the prefire lodgepole pine). Plots were located within ~ 4 km of one another such that environmental conditions other than burn status were similar.

Stand Characteristics

Stand structure and plant communities were sampled in July 2021; thus, time since fire (TSF) was

Table 1. Hypothesized Effects of Recent (5 ys postfire) Short-interval (SI, 16 y) Fire Relative to Long-interval (LI, > 130 y) Fire and Young (21-y-old) Postfire Forests that Did Not Reburn on Indicators of Nitrogen (N) Cycling in Subalpine Lodgepole Pine Forests of Grand Teton National Park, Wyoming

Response variable	Expected response	Rationale
Nitrogen stocks		
Live N pools	Lowest in SI fires, greatest in aggrading young forest	Postfire tree regeneration very low in SI vs LI fire; aggrading forest has high tree biomass and N stocks
Detrital N pools (litter, dead wood)	Lowest in SI fire, highest in aggrading young forest	Substantial combustion of downed coarse wood in SI fire, little accumulation of litter; abundant dead wood (down + standing) in LI fire; abundant litter in aggrading young forest
Mineral soil N pools	Soil N stocks lower in SI or no effect of fire	SI fires could have combusted some soil N during coarse wood smoldering or no effect because stand-replacing fires burn litter, but do not burn into mineral soil
Partitioning ratio (soil N: plant N)	Higher ratio for SI fire compared to LI fire; low ratio for the young aggrading forest	Live N pools would be lowest in the SI fire because plant N stocks would be smallest, leading to a higher ratio
Inorganic N availability		
Resin-sorbed N	No difference among burn categories or increased nitrate availability in SI fire	Microbial N sink is strong following high-severity fire; N consumption > N production in laboratory studies; negative net N mineralization in field studies, but low density of lodgepole pine litter more bare soil may leave more ammonium available for nitrification in SI fire
Correlation with postfire vegetation	Negative correlation with postfire lodgepole pine, positive correlation with herbaceous biomass or diversity	Prior studies indicate negative relationship between lodgepole pine biomass and productivity with available N; understory species respond positively if available N, especially nitrate, have increased
N fixation		
Symbiotic N fixation (*Lupinus argenteus*)	Greater abundance and N stock in Sl fires relative to LI fire or young forest that did not reburn	Lupines can establish after fire (resprouting followed by seedling establishment) and will benefit from high light and reduced competition in the reburns
Cryptic N fixation (moss, litter, soils)	Low rates in recent SI and LI fires, greater in aggrading forest that did not reburn	Cryptic fixers are more likely to be important after canopy closure and will not thrive in hot, dry conditions

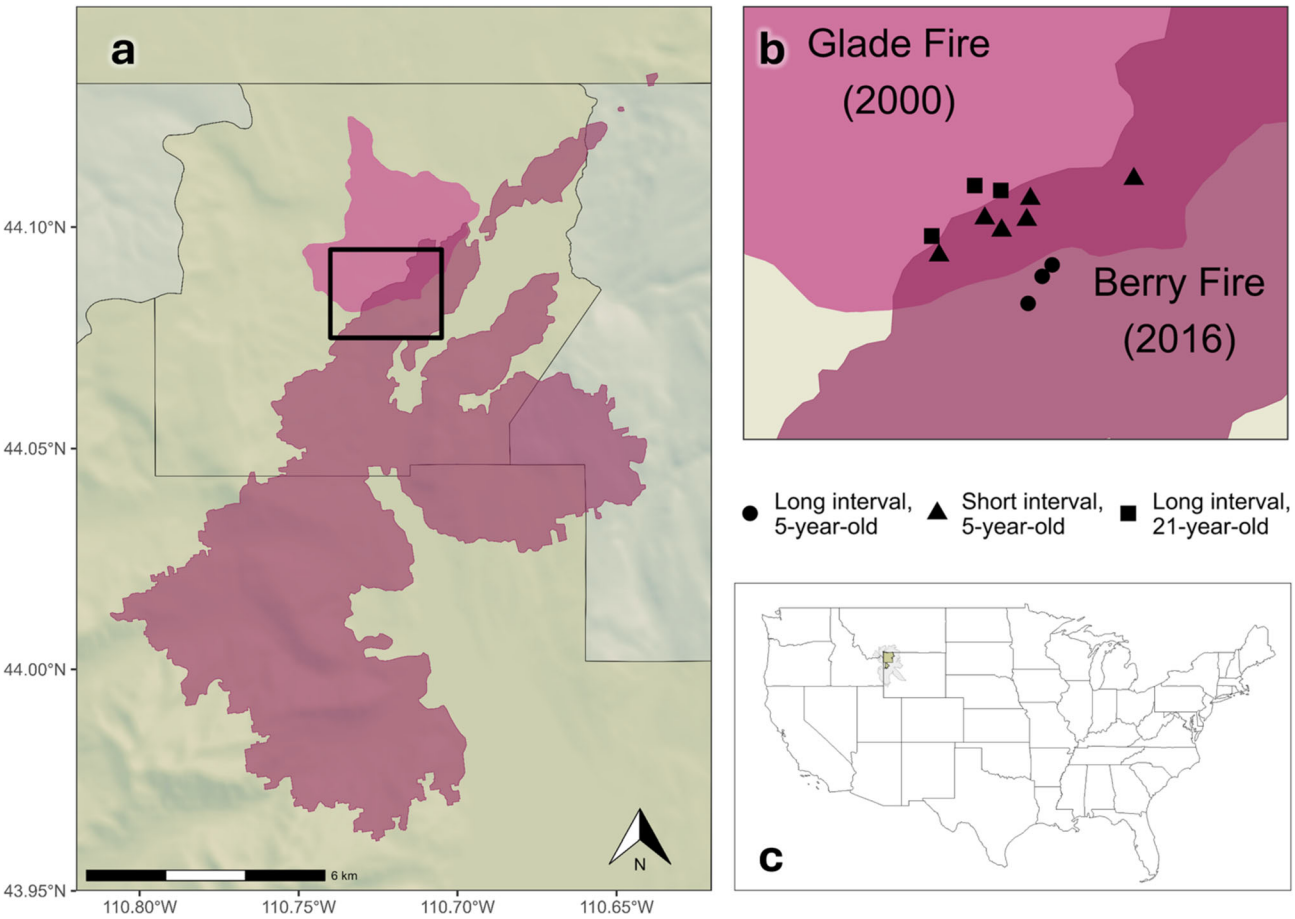

Figure 2. Study area map. **a** Extent of the 2000 Glade Fire (light pink) and 2016 Berry Fire (dark pink) and their overlap in Grand Teton National Park, Wyoming. **b** Plot locations within each fire, including those burned in the Glade Fire and not reburned (squares; $n = 3$), those burned in the Berry Fire and not burned previously for $>$ 130 years (circles; $n = 3$), and those burned in both the Glade and Berry Fire at a short fire return interval (triangles; $n = 6$). **c** Location of the Greater Yellowstone Ecosystem within the contiguous United States.

5 years for the nine plots burned in the Berry Fire and 21 years for the three plots regenerating after the Glade Fire. We tallied all postfire tree seedlings and aspen ramets in three 50 m × 2 m belt transects oriented to the north and separated by 25 m. At 5-m intervals along each transect, we located the nearest lodgepole pine and recorded its basal diameter and diameter at breast height (DBH) if height ≥ 1.37 m ($n = 25$ trees/plot). We also located the nearest aspen and recorded the number and height of each ramet emerging from a root crown. Because aspens were patchy within and among plots, we measured up to 25 aspens per plot based on their presence. Forest understory vegetation (graminoids, forbs, shrubs) was sampled by recording percent cover by species in 25 quadrats (0.50 m × 0.50 m) spaced at 5-m intervals along each transect. Percent cover of bare mineral soil, litter, moss and wood was also recorded in each quadrat.

Downed coarse wood (≥ 7.5 cm diameter) was measured in 2017 in the nine previously established plots in which fire-killed snags had already fallen (Turner and others 2019a), so we did not remeasure coarse wood in those plots in 2021. Most fallen dead trees remain elevated above the forest floor for many years, and decomposition is very slow until logs come in direct contact with the soil (Nelson and others 2016; Remsburg and others 2006). We sampled downed coarse wood in the three newly established plots using the same protocols. Measurements were taken along three 31.25-m Brown's transects (Brown 1974) oriented at azimuths of 0°, 120° and 240° to avoid potential

sample bias from non-random orientation of logs. Decay class (1–5, from sound to rotten) was also recorded for each log. Because fire-killed trees were still standing in these three plots (TSF = 5 years), we counted all snags rooted within each 50 m × 2 m belt transect by species and recorded the DBH of the nearest snag at each 5-m interval (n = 25 snags).

Organic N Concentrations and Stocks

N concentrations Litter and soils were sampled in July 2021. Each plot was subdivided into four 25 m × 25 m quadrants. At 3 m from each quadrant centroid in three sub-cardinal directions (northeast, southeast and southwest; n = 12 per plot), we collected a mineral soil core (2 cm diameter × 15 cm depth) and all aboveground litter within a 30 cm × 30 cm quadrat frame. Litter samples were air-dried in the field, returned to the laboratory and dried at 60°C to constant mass, and the mass was recorded. Litter was homogenized by quadrant and coarsely ground using a coffee grinder, then subsamples were finely ground and further homogenized prior to chemical analyses. Soil samples were composited by quadrant, sieved (2 mm), air-dried in the field and returned to the laboratory. Soil samples were then homogenized, subsampled and ground to a fine powder. Litter and soil samples were analyzed for C and N content on a Thermo Flash EA 1112 analyzer (Jackson Lab, University of Wisconsin-Madison, Madison, WI). In July 2023, we revisited each plot to measure soil bulk density by collecting a mineral soil core (5 cm diameter × 15 cm depth) from each quadrant. Samples were dried at 105°C and weighed to obtain bulk density estimates, then sieved and weighed again to obtain fine fraction (< 2 mm diameter) density.

Foliar N was sampled in July 2022. For trees, we collected fully emerged foliage from eight lodgepole pines in each plot (two in each quadrant) and, when present, from eight distinct aspen ramets in each plot. We identified a lodgepole pine representative in size of the dominant postfire cohort located three to four meters to the northeast and southwest from the centroid of each quadrant. We harvested a branch from the upper, middle and lower third of the canopy of each tree, selecting branches exposed to sun when possible. For very small lodgepole pines (for example, 5-year-old stems), all foliage was collected from each individual. Foliage was removed from each branch and placed in paper bags by tree, and woody material was discarded. A similar procedure was followed for aspens, but we could not always sample two ramets per quadrant because of their patchy distribution. For the understory vegetation, we identified the five most abundant species in each plot from the 2021 percent cover data. For each of these species in each plot, we collected all aboveground biomass (most of which was foliage) from at least five individuals. Samples were composited by species in each plot. All foliage samples were air-dried in the field then returned to the laboratory and prepared and processed for C and N analysis as described above for litter samples.

N stocks Nitrogen stocks (kg N ha^{-1}) were computed for each ecosystem component based on mass and N concentration as in Turner and others (2009, 2019a; b), and total ecosystem N stocks were estimated by summing individual stocks in each plot. For vegetation, we first applied locally developed age-class-specific allometric equations to predict live lodgepole pine biomass (Turner and others 2004; Copenhaver and Tinker 2014) and species-specific allometric equations to predict understory biomass from percent cover (Turner and others 2004). We developed new allometric equations for aspen ramets and four understory species not included in our prior studies (Appendix 1, Tables S1–S3).

For live lodgepole pine, the foliage N pool was estimated by multiplying foliage biomass (computed from allometric equations and stand density) by mean N concentration of the composite needles from the eight sampled trees. The aboveground woody N pool was estimated by computing branch and bole biomass from the allometric equations and using previously published N concentrations of 0.0035% for bole wood and 0.17% for branch wood (Fahey and others 1985) to estimate those N pools. Estimates were summed to obtain the total aboveground lodgepole pine N pool.

For aspen ramets, we similarly multiplied foliage biomass computed from allometric equations by the mean N concentration from the eight sampled ramets in each plot. We also predicted aboveground stem biomass for aspen, assumed 0.50 was C and the C:N ratio was 175 (deciduous broadleaf forest; Table S1, Cleveland and others 2013), and then multiplied stem biomass by 0.28% to estimate aspen stem N. Understory vegetation aboveground N pools were estimated by multiplying aboveground biomass by measured foliar N concentration for each of the five most abundant species in each plot then summing across those five dominant species.

Litter N pools were estimated by multiplying percent N by litter mass in each plot. For the mineral soil (0–15 cm) N pool, we averaged the four measurements of soil fine fraction (< 2 mm)

density (kg L^{-1}) in each quadrant, multiplied by soil percent N and reported stocks as kg N ha^{-1}. Nitrogen pools in downed coarse wood were estimated by applying published N concentration values to our estimates of coarse wood volume by decay class. For downed coarse wood, percent N was assigned at 0.065% for decay class 1, 0.085% for decay class 2 and 0.20% for decay classes 3–5 (Fahey 1983, Table 12). For the standing dead snags, we first estimated stem height (m) for each of the 25 measured snags by multiplying DBH (cm) by 0.80 for lodgepole pine and by 0.57 for subalpine fir based on height-to-diameter relationships derived from measurements of both species in our study area (Appendix 2, Figure S1). Stem biomass was estimated for each snag following Kashian and others (2013, Table 3) using the equation:

$$\text{Bole biomass} = 0.020 \times \text{DBH}^{1.535} \times \text{height}^{1.447} \quad (1)$$

where biomass is in dry kg, DBH is in cm and height is in m. The N content of each snag was estimated using 0.03% percent N for lodgepole pine heartwood (Fahey and others 1985). We calculated the mean N stock (kg N) per bole by species then multiplied by the density of lodgepole pine or subalpine fir snags on each transect and averaged the three transects to obtain a plot mean.

For each plot, we calculated the partitioning ratio (soil N:aboveground plant N; Kranabetter and others 2016). Soil N included mineral soil, forest floor litter and dead wood (which would eventually be incorporated into the soil pool), and plant N included the sum of aboveground live plant N stocks.

Annual Inorganic N Availability

As an index of plant-available N, we incubated 16 mixed-bed ion exchange resin bags in each plot for one year (July 2021 to July 2022). Free resin bags are effective in remote settings and correlate well with more labor-intensive measurements of net N mineralization (Binkley and others 1986, 1992). Bags were constructed from undyed nylon stocking material and filled with 20 g of mixed-bed ion exchange resin beads (J. T. Baker). Resin bags were soaked in 2M KCl and rinsed with deionized water prior to deployment. We installed one resin bag in each cardinal direction at a distance of 2 m from each quadrant centroid. Bags were gently inserted into the soil at a 45° angle to a depth of ~ 5 cm using a pry bar and tethered with nylon fishing line to which a metal identification tag was affixed. Resin bags were retrieved in July 2022 and returned to the laboratory where they were rinsed in deionized water to remove any soil particles and extracted in 75 ml of 2M KCl in urinalysis cups. Cups were agitated for 1 h on a shaker table, and extracts were filtered (Whatman No. 1 filter) and frozen for subsequent analyses. Extracts were analyzed for NO_3^-–N and NH_4^+–N at the University of Wisconsin Soil and Forage Lab (https://uwlab.soils.wisc.edu/) on a Latchet Instruments autoanalyzer. Results were adjusted for the number of days of incubation and reported in μg N bag^{-1} day^{-1}. All analyses also included blanks for standardizing data and checking for sample contamination. Results are reported for annual resin-sorbed nitrate, ammonium and total N as well as relative nitrification (annual resin-sorbed nitrate / total annual resin-sorbed N).

N Fixation

We sampled N fixation in litter, soils and moss in July 2021 using a modified acetylene reduction assay based on Hardy and others (1968) to measure nitrogenase activity. We did not observe lichens in these plots, and wood was either sound or charred, so we were unable to measure N fixation in those niches. Samples of pine litter (Oi), mineral soil (0–2 cm) and moss crust (*Ceratodon purpureus)* were collected into 50-ml acrylic tubes from each quadrant of each plot and processed the same day. Samples were injected with acetylene (C_2H_2) gas to replace 10% of the tube headspace with C_2H_2 (generated via calcium carbide reaction with water). The headspace was mixed after injection, and samples were incubated for 18 to 24 h in a partially wooded stand at ambient temperature. After incubation, headspace samples were collected and stored in vacuum sealed serum vials for transport back to the University of Montana. C_2H_4 production was then measured using a Shimadzu GC-2014 equipped with a flame ionization detector (Shimadzu Inc., Kyoto, Japan).

Nitrogen fixation rates were calculated by assuming a theoretical conversion ratio of 3 mol C_2H_4:1 mol N_2 fixed (Soper and others 2021). Following incubation, litter and moss samples were oven-dried at 60°C for 72 h and soil samples at 105°C to obtain dry masses. We then paired fixation rates with plot-level cover of moss crust and plot-level litter mass to estimate the amounts of N being fixed by these niches. Soil N fixation rates were scaled up using the total area and mean fine fraction density of soils in each plot to a depth of 2 cm (Son 2001). Plot-level N fluxes from fixation in the three niches were then extrapolated on an

hourly basis to annual growing season estimates assuming constant fixation throughout the entire growing season (~ 4380 h) and reported per hectare.

Data Analyses

All analyses were performed at the plot level. Given the relatively small sample size (n = 12 plots), we computed means for each response variable by burn category and tested for differences among burn categories using a general linear model and a post hoc Tukey's HSD test (α = 0.05). We computed Spearman's rank order correlations to evaluate potential relationships between inorganic N availability and vegetation. All response variables were tested for normality. Prior to analysis, lodgepole

Table 2. Stand Characteristics for Plots that Burned as a Long-interval (LI, ≥ 130 years) Fire in 2016 (n = 3), a Short-interval (SI, 16 years) Fire in 2000 and 2016 (n = 6), and LI Fire in 2000 (n = 3) in Grand Teton National Park

Variable	Long-interval fire, 5-year-old	Short-interval fire, 5-year-old	Long-interval fire, 21-year-old
Postfire live lodgepole pine			
Density (stems ha^{-1})	172,600^{a} ± 19,441	3,261^{b} ± 1,545	16,367^{b} ± 9,726
Mean tree aboveground biomass			
Mean tree foliage (g tree^{-1})	3.79^{b} ± 0.67	5.33^{b} ± 1.52	1,708^{a} ± 903
Mean tree branch (g tree^{-1})	0.27^{b} ± 0.12	0.47^{b} ± 0.20	1,519^{a} ± 840
Mean tree stem (g tree^{-1})	4.58^{b} ± 0.64	6.08^{b} ± 1.59	475^{a} ± 2,503
Total aboveground biomass			
Foliage biomass (Mg ha^{-1})	0.67^{b} ± 0.16	0.01^{c} ± 0.00	13.24^{a} ± 1.86
Branch biomass (Mg ha^{-1})	0.05^{b} ± 0.02	0.00^{c} ± 0.0005	11.26^{a} ± 1.2
Stem biomass (Mg ha^{-1})	0.80^{b} ± 0.17	0.01^{c} ± 0.004	36.93^{a} ± 5.28
Postfire live aspen			
Ramet density (ramets ha^{-1})	20^{a} ± 58	2,406^{a} ± 917	1,122^{a} ± 235
Mean ramet aboveground biomass			
Mean ramet foliage (g ramet^{-1})	4.6^{b} ± 0.84	16.3^{a,b} ± 2.47	29.0^{a} ± 7.85
Mean ramet wood (g tree^{-1})	11.1^{b} ± 2.24	51.2^{a,b} ± 8.75	105.6^{a} ± 34.10
Total aspen aboveground biomass			
Foliage biomass (Mg ha^{-1})	0.0008 ± 0.0001	0.0409 ± 0.0155	0.0326 ± 0.0094
Woody biomass (Mg ha^{-1})	0.002 ± 0.0003	0.13 ± 0.05	0.12 ± 0.04
Understory percent cover, biomass, richness			
Live understory vegetation cover (%)	40.7^{a} ± 3.1	40.3^{a} ± 4.3	17.2^{b} ± 5.7
Lupinus argenteus	0.09^{b} ± 0.09	6.6^{a} ± 1.3	4.2^{a} ± 0.37
Forbs	6.9^{b} ± 2.1	17.0^{a} ± 2.2	7.3^{b} ± 0.73
Graminoids	13.8^{a} ± 8.0	15.4^{a} ± 4.7	6.6^{a} ± 2.8
Shrubs	19.9^{a} ± 6.5	8.0^{a} ± 3.4	3.3^{a} ± 3.0
Moss	15.0^{a} ± 7.8	16.6^{a} ± 3.2	11.0^{a} ± 2.9
Bare mineral soil cover	14.0^{a,b} ± 10.8	30.8^{a} ± 3.2	6.2^{b} ± 3.4
Litter cover	10.9^{b} ± 1.8	3.8^{c} ± 0.9	43.6^{a} ± 6.2
Total understory biomass (Mg ha^{-1})	2.13^{a} ± 0.47	1.87^{a} ± 0.27	0.89^{b} ± 0.40
Species richness	30.3^{b} ± 0.88	39.0^{a} ± 1.86	27.3^{b} ± 2.33
Dead coarse wood			
Downed coarse wood biomass (Mg ha^{-1})	14.5^{b} ± 6.5	25.4^{b} ± 5.4	69.3^{a} ± 10.0
Lodgepole pine snags (Mg ha^{-1})	100.0 ± 20.0	0 ± 0	0 ± 0
Subalpine fir snags (Mg ha^{-1})	15.8 ± 8.9	0 ± 0	0 ± 0
Forest floor litter			
Litter biomass (Mg ha^{-1})	0.69^{b} ± 0.23	0.28^{b} ± 0.06	6.36^{a} ± 0.68
Soil fine fraction bulk density (kg L^{-1})	0.81^{a} ± 0.04	0.71^{a,b} ± 0.03	0.60^{b} ± 0.02

All plots burned at high severity (that is, stand-replacing fire). Vegetation, soil and litter were sampled in 2021. Values are mean ± one standard error. Differences among means by burn class are indicated by letters (Tukey's HSD test, α = 0.05).

pine density, biomass components and foliar N stock; litter mass and N stock; N fixation rate; and resin-sorbed nitrate were $\log_{10}$-transformed; litter C:N ratio was square-root-transformed; and percent cover data were arcsine square-root-transformed. For resin-sorbed N, we also computed a *t*-test to compare the effects of the short vs. long fire interval in the 5-year-old stands. Means and standard errors are reported in actual units, but statistical differences were evaluated using transformed data when appropriate. Except for N fixation rate, which was analyzed using R (R Core Team 2023), analyses were conducted using SAS version 9.4 (SAS Institute 2023).

Results

Stand Characteristics

Stand structure varied among burn categories. Postfire lodgepole pine densities were two orders of magnitude lower in the short-interval fire compared to nearby areas that also burned in 2016 but as long-interval fire (Table 2). Furthermore, densities in the reburns were roughly five times lower than in stands that regenerated after the 2000 Glade Fire and did not burn again (Table 2). Aspens were patchily distributed; although ramet densities varied among burn classes (Table 2), differences were not significant. Aspen ramets were largest where they had established as seedlings after the 2000 Glade Fire and had not reburned; intermediate in size in the reburns, where they resprouted after the 2016 fire; and smallest in the most recent long-interval fire, where individuals were likely seedlings because aspen was not present in the mature forest prior to the 2016 fire (Table 2).

Live understory cover was greatest in the 5-year-old stands that burned as either short- or long-interval fire compared to the 21-year-old stands that had not reburned, and species richness was highest in the reburn (Table 2). Species richness was not correlated with aboveground understory biomass, but was negatively correlated with live lodgepole pine biomass (R_s = -0.82, p = 0.0009). Percent cover of forbs and bare mineral soil were greatest, and percent cover of litter was lowest in the short-interval fires (Table 2).

Biomass of downed coarse wood and forest floor litter was greatest in the young stands that did not reburn (Table 2). Predictably, forest floor litter mass was strongly positively correlated with live lodgepole pine biomass (R_s = 0.82, p = 0.0010), the primary source of litter in these forests. The total amount of dead wood (that is, standing plus downed coarse wood) was greatest in the recent long-interval fire (Table 2). Areas of short-interval fire had the least dead wood, and all dead wood was down.

Organic N Concentrations and Stocks

Lodgepole pine foliar N concentrations were substantially higher and foliar C:N ratios lower in the short-interval fire, where lodgepole pines were least dense, compared to either the recent long-interval burn or the 21-year-old stands that did not reburn (Table 3). Aspen foliar N concentrations were higher than in lodgepole pine, and aspen foliar N was greatest and C:N lowest in areas that burned in the 2000 fire, regardless of whether the stands had reburned (Table 3). Among understory herbaceous species, foliar N concentrations were highest in the symbiotic N fixer, *Lupinus argenteus* (ranging among plots from 3.28 to 5.47% N; Appendix 3, Table S4). Foliar N concentrations were generally lowest (ranging between 1 and 2% N) among graminoids, including *Carex rossii*, *Carex geyerii* and *Calamagrostis rubescens* (Appendix 3, Table S4). Most other forbs and the shrub, *Spirea betulifolia*, had foliar N concentrations between 2 and 3% N (Appendix 3, Table S4). Soil and litter N concentrations and C:N ratios did not vary among burn categories (Table 3).

Five years postfire, total aboveground N stocks were 117 ± 20.4 kg N ha^{-1} in areas of long-interval fire and only 81 ± 9.3 kg N ha^{-1} (31% lower) in areas of short-interval fire (Figure 3a). Lodgepole pine foliar N stocks were 44 × greater in the long- versus short-interval fire (Table 3), reflecting drastic difference in postfire tree density and foliar biomass (Table 2). Deadwood N stocks were nearly double in areas of long- vs. short-interval fire (62 ± 11.8 vs. 37 ± 6.7 kg N ha^{-1}, respectively), litter N stocks were higher (7.05 ± 2.72 vs. 2.61 ± 0.68 kg N ha^{-1}, respectively), and understory N stocks were comparable (∼ 40 kg N ha^{-1}; Figure 3a and Table 4). By contrast, aboveground N stocks were much greater (327 ± 20.5 kg N ha−1) in 21-year-old stands that did not reburn (Figure 3b). In these aggrading stands, deadwood and litter N stocks were also high (82.3 ± 6.7 and 56.3 ± 6.8 kg N ha^{-1}, respectively), but herbaceous N stocks were considerably lower (18.6 ± 8.3 kg N ha^{-1}; Figure 3b). Thus, aboveground N stocks were 78% lower in short-interval fire relative to the stands that did not reburn. However, aboveground N stocks in aspen that resprouted after the short-interval fire averaged 1.44 ± 0.53 kg N ha^{-1}, nearly an order of magni-

Table 3. Nitrogen Concentrations, C:N Ratios and N Stocks for Tree Foliage, Litter and Soils in Plots that Burned as a Long-interval (LI, ≥ 130 ys) Fire in 2016 (n = 3), a Short-interval (SI, 16 years) Fire in 2000 and 2016 (n = 6), and LI Fire in 2000 (n = 3)

Variable	Long-interval fire, 5-year old	Short-interval fire, 5-year-old	Long-interval fire, 21-year-old
Lodgepole pine foliar N			
Foliar N (composite needles; %)	$1.19^{b} \pm 0.06$	$1.82^{a} \pm 0.10$	$1.05^{b} \pm 0.07$
Foliar C:N (composite needles)	$46.8^{b} \pm 2.07$	$29.5^{a} \pm 1.56$	$53.2^{b} \pm 2.87$
Foliar N stock (kg N ha^{-1})	$7.9^{b} \pm 2.01$	$0.18^{c} \pm 0.06$	$136.7^{a} \pm 10.02$
Aspen foliar N			
Foliar N (%)	$2.01^{a} \pm 0.08$	$2.67^{b} \pm 0.13$	$2.63^{b} \pm 0.19$
Foliar C:N	$26.9^{a} \pm 1.19$	$19.8^{b} \pm 0.92$	$20.2^{b} \pm 1.46$
Foliar N stock (kg N ha^{-1})	$0.017^{b} \pm 0.003$	$1.08^{a} \pm 0.40$	$0.89^{a} \pm 0.30$
Forest floor litter			
Litter N (%)	$1.0^{a} \pm 0.07$	$0.92^{a} \pm 0.07$	$0.90^{a} \pm 0.02$
Litter C:N ratio	$49.5^{a} \pm 2.40$	$48.3^{a} \pm 2.90$	$53.9^{a} \pm 6.75$
Litter N stock (kg N ha^{-1})	$7.0^{b} \pm 2.72$	$2.6^{b} \pm 0.68$	$56.3^{a} \pm 6.75$
Mineral soil			
Soil N (%)	$0.09^{a} \pm 0.00$	$0.10^{a} \pm 0.02$	$0.12^{a} \pm 0.01$
Soil C:N ratio	$21.3^{a} \pm 1.4$	$20.3^{a} \pm 0.67$	$21.7^{a} \pm 1.14$
Soil N stock (0–15 cm; kg N ha^{-1})	$1{,}073^{a} \pm 18$	$1{,}077^{a} \pm 130$	$1{,}060^{a} \pm 50$

All plots burned at high severity (that is, stand-replacing fire). Soil and litter were sampled in 2021. Live foliage for N concentrations was collected in 2022. Values are mean ± one standard error. Differences among means indicated by letters (Tukey's test, α = 0.05).

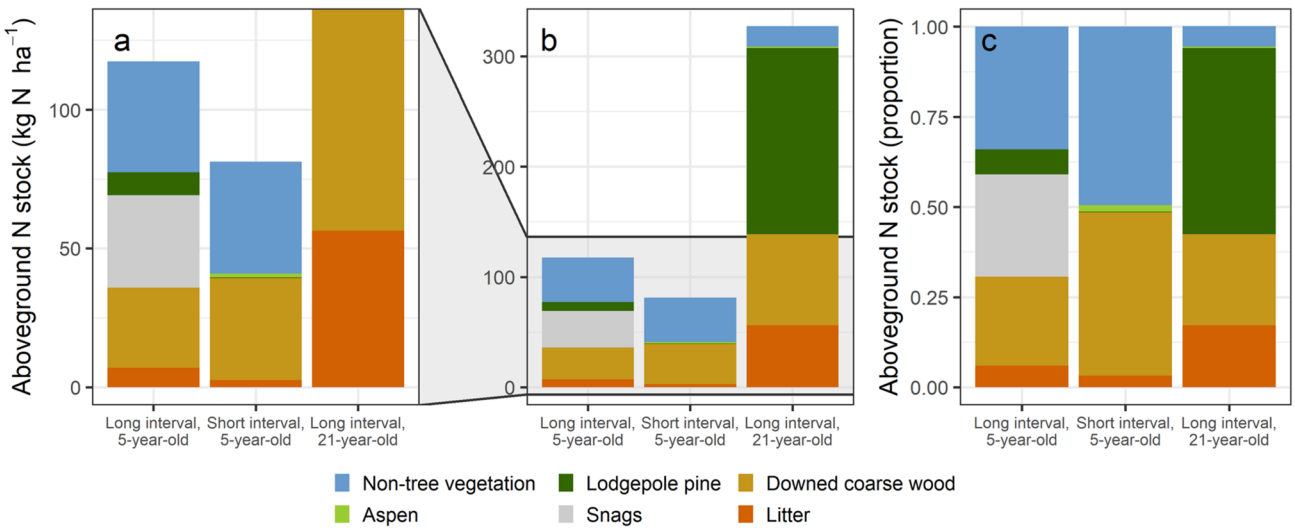

Figure 3. Total aboveground N stocks (kg N ha^{-1}) in each ecosystem component by burn class, with y axis scaled to the 5-yr old long- and short-interval fires (**a**) or to include the 21-yr old long-interval fire (**b**); and as proportions of total aboveground N stocks (**c**).

tude greater than lodgepole pines (0.19 ± 0.06 kg N ha^{-1}) and comparable to N stocks in the 21-year-old stands (1.22 ± 0.41 kg N ha^{-1}) where aspen established from seed after the 2000 fire.

Proportional allocation of aboveground N stocks varied markedly among burn categories (Figure 3c). At 5 years postfire in the short-interval fire, 49% of the aboveground N stock was in understory vegetation and 45% in downed coarse

Table 4. Foliar N Concentration, Aboveground Biomass and Aboveground N Stocks for *Lupinus argenteus* and Total Aboveground N Stocks in Understory Vegetation

Response	Long-interval fire, 5-year-old	Short-interval fire, 5-year-old	Long-interval fire, 21-year-old
Lupinus argenteus			
Foliar N concentration (%)	0 ± 0	4.01 ± 0.17	4.42 ± 0.53
Aboveground biomass (Mg ha)	0 ± 0	0.15 ± 0.03	0.10 ± 0.01
N stock (kg N ha^{-1})	0 ± 0	6.00 ± 1.04	4.23 ± 0.35
Total aboveground understory N stock (kg N ha^{-1})	38.9^{a} ± 8.9	40.2^{a} ± 4.73	18.6^{b} ± 8.3

Values indicate mean and one standard error. Differences among means indicated by letters (Tukey's test, α = 0.05).

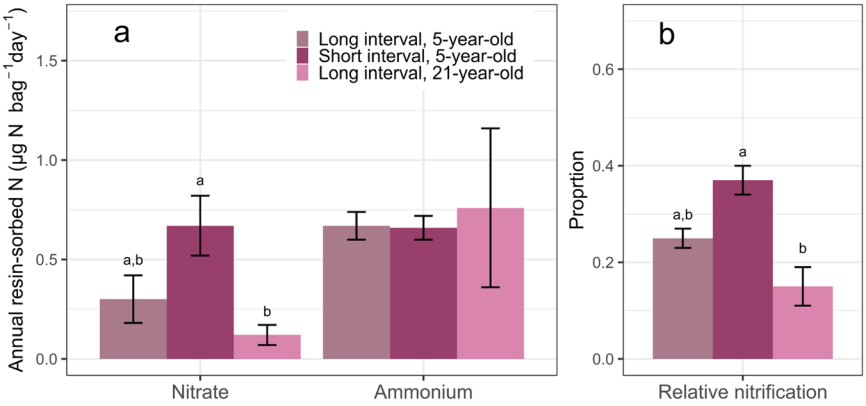

Figure 4. Resin-sorbed nitrate and ammonium (µg N bag^{-1} day^{-1}) by burn class from year-long incubation of resin bags (**a**) and relative nitrification (**b**). Error bars indicate ± one standard error.

wood (Figure 3c). In the long-interval fire, only 34% of the aboveground N stock was in understory vegetation and 53% was in the dead wood pools (Figure 3b). In 21-year-old forests that did not reburn, 52% of the aboveground N was in live tree biomass followed by 25% in downed coarse wood and 17% in forest floor litter; only 6% was in the understory vegetation (Figure 3c).

Soil N stocks (0–15 cm) averaged 1,072 ± 63 kg N ha^{-1} and did not vary among burn categories (Table 3). Total ecosystem N (aboveground + soil N) averaged 1,235 ± 71 kg N ha^{-1} and did not vary with burn category. Soil N accounted for 86% of total ecosystem N.

The N partitioning ratio (soil N: aboveground plant N) did not differ between short- and long-interval fire at 5 years postfire (28.2 ± 4.2 and 25.0 ± 5.3, respectively). However, the N partitioning ratio was lower and less variable in the 21-year-old aggrading forest that did not reburn (5.2 ± 0.4) as live plant N stocks (the denominator) increase with time since fire.

Annual Inorganic N Availability

Total annual resin-sorbed N and resin-sorbed ammonium averaged 1.13 ± 0.14 and 0.69 ± 0.09 µg N bag^{-1} day^{-1}, respectively, and neither varied with burn category (Figure 4). However, annual resin-sorbed nitrate and relative nitrification were highest in areas of short-interval fire (0.67 ± 0.15 µg N bag^{-1} day^{-1} and 37% ± 3%, respectively) and lowest in the 21-year-old forest that did not reburn (0.12 ± 0.05 µg N bag^{-1} day^{-1} and 15% ± 4%, respectively) (Figure 4). When comparing only the 5-year-old stands that burned at long vs. short fire interval, relative nitrification rates were higher in the short-interval fire ($t = -3.25$, df = 7, $p = 0.0148$).

Annual resin-sorbed nitrate was positively correlated with understory species richness ($R_s = 0.76$, $p = 0.0041$), biomass ($R_s = 0.59$, $p = 0.0446$) and aboveground N stocks ($R_s = 0.62$, $p = 0.0332$) and negatively correlated with litter mass and litter N stock ($R_s = -0.77$, $p = 0.0040$ and $R_s = -0.77$, $p = 0.0034$, respectively). Live lodgepole pine bio-

mass and N stocks were negatively correlated with annual resin-sorbed nitrate ($R_s = -0.83$, $p = 0.0010$), relative nitrification ($R_s = -0.71$, $p = 0.0092$) and total annual resin-sorbed N ($R_s = -0.59$, $p = 0.0446$; rank order of plots was the same for both lodgepole pine variables). Downed coarse wood biomass and N stocks and total ecosystem N stocks were unrelated to resin-sorbed N.

N Fixation

The symbiotic N fixer *Lupinus argenteus* was uncommon in our plots (< 7% cover; Table 2), and biomass and aboveground N stocks were similar in areas that burned in 2000, regardless of whether these did or did not reburn (Table 4). Symbiotic N fixers were nearly absent in the 5-year-old stands that burned as long-interval fire (although *Shepherdia canadensis*, also an N fixer, was present at 3.7% cover in one plot; Appendix 3, Table S4).

Acetylene reduction rates measured in asymbiotic (cryptic) organisms in July 2021 were consistently low across all niches. Mean rates ranged from 0.016 nmol C_2H_4 g^{-1} h^{-1} in litter and moss to 0.003 nmol C_2H_4 g^{-1} h^{-1} in soil, but acetylene reduction rates were not significantly different among niches. When scaled to annual N fixation rates, N fixation was greater in mineral soil (0.051 ± 0.01 kg N ha^{-1} y^{-1}) than in litter (0.005 ± 0.003 kg N ha^{-1} y^{-1}) or moss (0.023 ± 0.015 kg N ha^{-1} y^{-1}), but rates in all niches were < 0.1 kg N ha^{-1} y^{-1}. There were no differences in summer scaled N fixation rates among the three burn categories (Figure 5). Together, estimates indicate that cryptic fixers contribute 0.079 ± 0.013 kg N ha^{-1} y^{-1}.

Discussion

This study found that a novel short-interval high-severity fire had relatively subtle effects on the N economy of subalpine lodgepole pine forests in the GYE. Aboveground N stocks declined sharply and partitioning among aboveground pools was substantially altered, but short-interval fire did not initiate the hypothesized ratchet decline in total ecosystem N stocks (Figure 1) because the large soil N pool buffered the ecosystem from net declines. The N partitioning ratios suggested high resistance of ecosystem N stocks to short-interval fire. Coarse wood, a key component of the C cycle, played a surprisingly small role in the N balance of these postfire stands due to the low N concentration of wood. Nitrification rates remained elevated five years after short-interval fire and may have enhanced opportunities for more herbaceous species to establish. With reduced tree density, herbaceous biomass could remain high in the reburns and reinforce elevated rates of nitrification. Rates of asymbiotic N fixation were low. However, while *Lupinus argenteus* was not abundant, its presence in all plots suggests it could play some role in postfire N replenishment. Overall, however, short-interval fires had greater effects on vegetation structure and C stocks (Turner and others 2019a; b) than on ecosystem N stocks and fluxes.

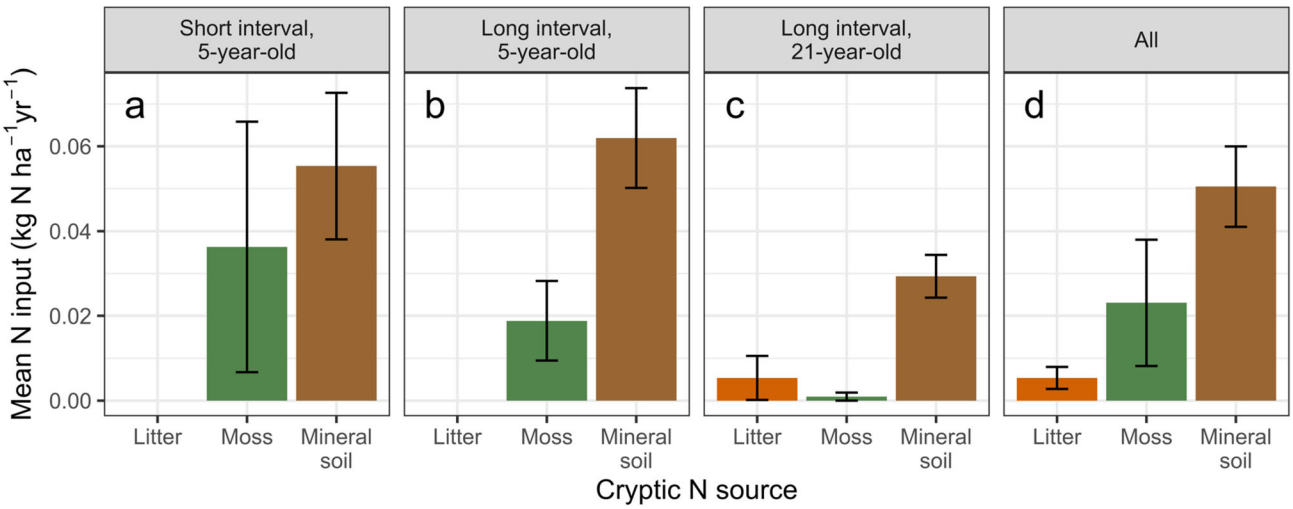

Figure 5. Mean rates of asymbiotic nitrogen fixation measured in three cryptic niches during summer 2021 by burn class (**a–c**) and across all 12 plots for each cryptic niche (**d**). Error bars represent ± one standard error.

Organic N Concentrations and Stocks

Foliar and litter N concentrations were similar to ranges reported in other studies (for example, Moore and others 2004; Litton and others 2004; Turner and others 2019b). The high lodgepole pine foliar N concentrations in the reburns are consistent with individual trees having higher foliar N when growing in less dense stands (Turner and others 2009). Further, the 1.81% foliar N was comparable to the 1.87% reported for four-year-old lodgepole pine seedlings that regenerated after the Glade Fire (Romme and others 2009), suggesting nutrient uptake processes were similar in the long- and short-interval fire. We suspect that the lower foliar N concentrations in the long-interval 2016 Berry Fire reflects a dilution effect (Binkley 1986), as we have seen in other postfire lodgepole pine stands (Turner and others 2009) due to the very high density of postfire lodgepole pine seedlings ($> 170{,}000$ ha^{-1}).

As hypothesized, live and detrital N pools were lowest in the reburns, consistent with sparse postfire tree regeneration and high combustion of woody fuels (Turner and others 2019a). However, the short-interval fire did not reduce total N stocks because mineral soils contained $> 80\%$ of ecosystem N, consistent with patterns of ecosystem N storage in northwestern US forests (Page-Dumroese and Jurgensen 2006). Other studies have also revealed resistance of total ecosystem N stocks to aboveground disturbance. For example, a chronosequence study of Siberian Scots pine (*Pinus sylvestris*) in which 75% of total N was in the mineral soil found no effect of stand age, fire regime and site type on ecosystem N (Wirth and others 2002). Experimental manipulations involving fire and fire surrogate treatments in western conifer forests also never affected more that 10–15% of total N, again because soil total N was unresponsive to treatment (Boerner and others 2008). Pellegrini and others (2018) reported that fire-driven N losses were not substantial in temperate and boreal needleleaf forests. Although our study found strong influences on non-soil N stocks that may be ecologically important for N cycling, a novel short-interval fire did not affect total ecosystem N stocks.

Coarse wood, which is a key component of the C economy, played less of a role in the N economy of these forests, at least in the short term. While fuel combustion was high in the short-interval fire, the N content of wood is relatively low. Coarse wood similarly did not contribute substantially to N and P cycling in three Rocky Mountain conifer forests due to low N content and slow decay rates (Laiho and Prescott 1999). In a 30-year experimental study in the Canadian Rocky Mountains, net release of N from decomposing lodgepole pine logs occurred only after logs had lost 90% of their original C and the C:N ratio declined to < 200 (Prescott and others 2017). However, the absence of snags as a source of downed coarse wood following short-interval fires could reduce sites for N replenishment via N fixation over the long term.

The similarity of N partitioning ratios (~ 26) in short- and long-interval burns at five years postfire suggests that ecosystem N stocks in these subalpine lodgepole pine forests are insensitive to FRI in the short term. Using N data from a chronosequence in Yellowstone (Smithwick and others 2009), the average N partitioning ratio for a mature 200-year-old lodgepole pine stand is ~ 5.0. The aggrading lodgepole pine stands in our study reached this ratio within 21 years postfire, suggesting fast recovery of the partitioning ratio when aboveground plant N increases with robust postfire tree regeneration. However, rates of return to prefire values may diverge in the future if recovery of plant N is slow in the reburns due to sparse tree regeneration. Modest proportional losses of N to combustion may also confer resistance of ecosystem N stocks to reburns. We cannot directly compute the stability ratio (N removed: N stored; Himes and others 2014) for the recently burned stands, but we can estimate this ratio for 15-year-old postfire lodgepole pine stands assuming that forest floor litter N and live foliage N were combusted by fire (data in Turner and others 2019b). Himes and others suggest that forests with stability ratios < 0.1 are at low risk for nutrient depletion, whereas forests with ratios > 0.3 have significant risk. Using mean values from 14 postfire stands (Turner and others 2019b) to estimate N removed by fire in 15-year-old stands, a stability ratio of 0.087 indicates that these forests are at low risk for N depletion because the ecosystem N stored in the mineral soil far exceeds N lost to short-interval fire.

Annual Inorganic N Availability

Our hypothesis that total inorganic N availability would not differ among burn categories was supported, but nitrification rates were elevated in the short-interval fire. Elevated nitrification could be a legacy of burn severity, reflecting the greater combustion of coarse wood and prevalence of 'ghost logs' in the reburns (Turner and others 2019a) with effects similar to those of slash pile burn scars, in which extractable nitrate was

1.8 × higher than in unburned forest soils (Rhoades and others 2021). The positive correlation between resin-sorbed nitrate and understory species richness and biomass was intriguing. We cannot determine whether increased available nitrate promoted a more diverse assemblage or whether diverse litter sources promoted nitrification. However, N additions to mixed-conifer understory plant communities in the Sierra Nevada unexpectedly increased species richness (Hurteau and North 2008), and we suspect that elevated nitrate concentrations could have allowed a larger suite of species to establish. Furthermore, herbaceous and aspen biomass is likely to remain high in reburns given the sparse density of lodgepole pines. In turn, N cycling rates could accelerate via uptake of inorganic N and production of litter with relatively high N concentrations that may be more easily decomposed than relatively N-poor pine needles (Aerts 1997).

The negative correlation between lodgepole pine live biomass and resin-sorbed N is consistent with other studies in the GYE and with the observation that lodgepole pine is not limited by available N during early decades of postfire succession (Turner and others 2009, 2019a; b). Lodgepole pine is associated with ectomycorrhizal fungi that readily colonize first-year seedlings (Miller and others 1998), and it may rely solely on this symbiosis to access N and other critical resources. The relationship between soil N availability and canopy nutrition of *Pinus ponderosa* stands was also weak, as soil nutrient pools were poorly correlated with nutrient uptake and not useful for predicting stand productivity (Wilson and Maguire 2009).

N Fixation

Short-interval fire did not alter rates of N fixation in these stands, and our hypotheses were only partially supported. When *Lupinus argenteus* is present, high tissue N concentrations suggest the potential for symbiotic fixation to contribute some new N to the ecosystem. *Lupinus* influences N availability via root exudates while actively growing and via N-rich litter when plants senesce (Goergen and others 2009). While *Lupinus argenteus* is capable of fixing N on high-elevation sites in the Rocky Mountains (Johnson and Rumbaugh, 1986), maximum fixation rates for high-density lupine patches in Wyoming lodgepole pine forests were estimated at only 0.01 kg N ha^{-1} y^{-1} (Fahey and others 1985). Fixation rates of *Lupinus* species on successional volcanic sites at Mount St. Helens were similarly very low (< 0.05 kg N ha^{-1}; Halvorson and others 1992). Lupines resprout after fire and fill in locally (Turner and others 1997), but given their large heavy seeds, their distribution remains patchy (Romme and others 2016).

Our hypothesis that asymbiotic N fixation would be low in all recently burned (5 years postfire) stands was supported, but we were surprised to see such low values of asymbiotic N fixation in the rapidly growing 21-year-old lodgepole pine stands. Light conditions in these stands may still have favored symbiotic N fixers because the canopy had not yet closed. Our measurements were also taken during midsummer, when dry conditions may have constrained asymbiotic fixation. Low rates of cryptic fixation may reflect frequent asynchrony between the favorable temperature and moisture conditions that would be needed to sustain asymbiotic fixation (Heumann and others 2025). However, our estimates are conservative, considering only the upper 2 cm of mineral soil, so rates could be higher if deeper soils were also active.

Based on average N stocks in 15-year-old postfire lodgepole pine foliage and forest floor litter (46 and 28.6 kg N ha^{-1}, respectively; Turner and others 2019b), we estimate that approximately 75 kg N ha^{-1} was released to the atmosphere in the 2016 reburn. Given low rates of atmospheric deposition (< 2 kg N ha^{-1} y^{-1}) in our study area, additional annual inputs of ~ 3 kg N ha^{-1} y^{-1} via symbiotic and asymbiotic N fixation could replenish this lost N in as little as 15 years. However, the inputs we measured are much lower and cannot explain the increase in N stocks reported for aggrading postfire lodgepole pine forests (Turner and others 2019b).

Caveats

Results of this study may not apply to drier forest types (for example, *Pinus ponderosa*) characterized by frequent low-severity fires or boreal forests with deep organic soils. We also studied a single compound fire event, and others have postulated that repeated N losses due to subsequent fires could affect long-term soil productivity if N-fixing plants did not establish (Newland and DeLuca 2000; Page-Dumroese and Jurgensen 2006). The interplay between fire severity, fire return interval, N combustion and N availability may become more important to ecosystem productivity and postfire succession if fires continue to reburn the same sites multiple time (Harden and others 2002).

Conclusions

Novel short-interval fire drastically altered postfire forest structure in the forests we studied, but effects on the N economy were subtle. The large mineral soil N pool buffered subalpine lodgepole pine forests from effects of N losses via combustion, and the symbiosis of lodgepole pines with N-acquiring ectomycorrhizal fungi suggests that fire-driven N losses may be inconsequential for tree productivity. Additional short-interval fires could further change these ecosystems if effects compound in the future (Hayes and Buma 2021). Tree regeneration is likely limited by other factors (for example, seed supply, microclimate), and N is unlikely to pose strong constraints unless repeated short-interval fires induce chronic N losses in the future. However, substantial changes in the amount and partitioning of aboveground N stocks and elevated nitrification suggest that short-interval fire may have a persistent influence on N turnover and cycling.

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DATA AVAILABILITY

Data are available at: Turner, M.G., R.E. Heumann, N.G. Kiel, J.A. Warren and C.C. Cleveland. 2024. Data for: Reburning before recovery: Effects of short-interval fire on subalpine forest nitrogen stocks and fluxes ver 1. Environmental Data Initiative. https://doi.org/https://doi.org/10.6073/pasta/6de0219e436f62352b383be70d74b7d9 (Accessed 2024–11-20).

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