

Long-Term Nitrogen Storage and Soil Nitrogen Availability in Post-Fire Lodgepole Pine Ecosystems

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ABSTRACT

Long-term, landscape patterns in inorganic nitrogen (N) availability and N stocks following infrequent, stand-replacing fire are unknown but are important for interpreting the effect of disturbances on ecosystem function. Here, we present results from a replicated chronosequence study in the Greater Yellowstone Ecosystem (Wyoming, USA) directed at measuring inorganic N availability (ion-exchange resin bags) and ecosystem N pools among 77 lodgepole pine stands that varied in age and density. Inorganic N availability ranged from 0.07 to 3.20 $\mu\text{N bag}^{-1} \text{d}^{-1}$ and nitrate (NO_3^-) was, on average, 65% of total resin-sorbed N. Total ecosystem N stocks (live + detrital + soil) averaged $109.9 \pm 3.0 \text{ g N m}^{-2}$ (range = 63.7–185.8 g N m^{-2}). Live N was 14%, detrital N was 29%, and soil N was 57% of total stocks. Soil NO_3^- , total ecosystem N, live N, and detrital N generally increased with stand age, but soil N stocks decreased. Models (AIC_c) to predict soil N availability and N stocks included soil P, soil Ca, bulk density, and pH in

addition to age (adj R^2 ranged from 0.18 to 0.53) and density was included only for live N stocks. Patterns of N stocks and N availability with density were strongest for young stands (<20 years) regenerating from extensive fire in 1988; for example, litterfall N stocks increased with density (adj $R^2 = 0.86$, $P < 0.001$) but inorganic N availability declined (adj $R^2 = 0.47$, $P < 0.003$). Across the complex Yellowstone landscape, we conclude that N stocks and N availability are best predicted by a combination of local soil characteristics in addition to factors that vary at landscape scales (stand density and age). Overall, total ecosystem N stocks were recovered quickly following stand-replacing fire, suggesting that moderate increases in fire frequency will not affect long-term landscape N storage in Greater Yellowstone.

Key words: nitrate; ammonium; chronosequence; succession; density; yellowstone; *Pinus contorta*.

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INTRODUCTION

Nitrogen (N) cycling changes dramatically as succession proceeds (Vitousek and Reiners 1975) and may at least partially elucidate age-related declines in forest productivity (Gower and others 1996; Murty and others 1996). Following fire, N

availability is generally high due to elevated N mineralization (Wan and others 2001), which may result from favorable temperature and moisture conditions, low plant uptake, tendency for presence of N-fixing vegetation, and the deposition of charcoal that may absorb phenolics (Deluca and others 2006). However, little is known about the legacy of stand-replacing fires on patterns of long-term ecosystem N cycling (Smithwick and others 2005). A lack of replicated chronosequence studies has precluded understanding of how N patterns differ across fire-disturbed landscapes even though variation in landscape stand-age mosaics are critical for calculating landscape carbon (C) flux (Pregitzer and Euskirchen 2004; Smithwick and others 2006).

In this study, we were interested in exploring whether general patterns of soil N availability and ecosystem N stocks would be evident across a complex post-fire landscape that varies in stand age and tree density. The Greater Yellowstone Ecosystem (GYE, Northwestern Wyoming, USA) is characterized by stand-replacing fires that occur approximately every 100–300 years (Romme 1982) and create a landscape stand-age mosaic, providing an opportunity to explore long-term patterns in N cycling across a broad extent. Previous work in lodgepole pine ecosystems in the Rocky Mountains has shown that annual net N mineralization rates measured in situ decreased with time since fire (Turner and others 2007), whereas inorganic N availability has been shown to slightly increase or not change with stand age (Ryan and Waring 1992). Fewer studies have explored patterns in N stocks following fire. Although fire is known to decrease organic N pools via combustion, recent work suggests that combustion N losses from severe fires may be small, less than 1–6% of total prefire N (Page-Dumroese and Jurgensen 2006). Because lodgepole pine productivity is considered to be limited by N availability (Fahey and Knight 1986), understanding the long-term consequences of fire on soil N availability and N stocks across complex landscapes remains a key unknown. In this study, we asked: *how do inorganic soil N availability and total ecosystem N stocks vary with time since fire?* Previous modeling efforts have shown that C and N stocks recovered quickly (between 70 and 100 years) relative to the average fire return interval (Kashian and others 2006; Smithwick and others 2009). Therefore, we expected total ecosystem N stocks measured in the field to be lowest among young stands recovering from fire (<100 years), but not to differ among mature stands. However, trends in inorganic N availability with stand age are

conflicting, with at least one study in lodgepole pine showing increases (Olsson and others 1997) and another showing decreases (Turner and others 2007). To explore these patterns, we investigated ecosystem N stocks (live + detrital + soil) and soil N availability (measured with annual in situ resin bags) in the GYE along a replicated chronosequence ($n = 77$ stands) of lodgepole pine (*Pinus contorta* ssp. *latifolia* [Engelm. Ex Wats. Critchfield]) forests that varied in stand age from 12 to 331 years.

In addition to patterns in stand age, the 1988 fire in Yellowstone National Park (YNP) created a landscape stand-density mosaic, providing an opportunity to explore variation in inorganic N availability across stands that varied in density. Specifically, tree (>4 cm dbh) density ranged from 0 to 535,000 stems (saplings + trees) per hectare because of variation in pre-fire serotiny and fire severity in forests that burned in the extensive 1988 fires (Kashian and others 2004; Turner and others 2004). Differences in tree density following severe fire appear to persist for approximately 200 years followed by convergence to similar tree density among older stands (Kashian and others 2005). Thus, we also asked: *how do patterns in ecosystem N stocks and inorganic N availability vary with post-fire density?* Previous work (Litton and others 2004; Levitt 2006) has indicated lower summer inorganic N availability among dense versus sparse stands 12–15 years following the 1988 fires, but these patterns have not been evaluated across the range of stand densities and ages across the GYE. We expected that stands with higher stem densities (trees + saplings) would have lower inorganic soil N availability because N is considered to limit ecosystem productivity in lodgepole pine forests in the western United States (Fahey and Knight 1986). We also expected that, in general, stands of lower density would have lower total N stocks.

The degree to which fires modify ecosystem N storage is likely to result from complex interactions between fire severity and landscape location (Wirth and others 2002; Harden and others 2002; Bond-Lamberty and others 2006). However, effect of site variation on landscape-scale patterns in N cycling has not been previously evaluated across temperate ecosystems following stand-replacing fire. Therefore, to further understand the complex site conditions that are likely to modify N cycling, we aimed to develop statistical models for predicting soil N availability and ecosystem N stocks based on soil characteristics in addition to variation in stand age and tree density.

METHODS

Site Description

Yellowstone National Park is part of the GYE and is located on high-elevation forest plateaus in north-west Wyoming. The current forested elevation ranges from 1,900 to 2,900 m (Romme and Turner 1991). Approximately 80% of the park is dominated by lodgepole pine (*Pinus contorta*) forest, but subalpine fir (*Abies lasiocarpa* (Hook.) Nutt.), Engelmann spruce (*Picea engelmannii* Parry), whitebark pine (*P. albicaulis* Engelm.), and Douglas-fir (*Pseudotsuga menziesii*) may be locally abundant. Understory communities in YNP are generally dominated by resprouting perennials, with fire-intolerant perennials increasing in stands with longer fire intervals (Schoennagel and others 2004). Annual average precipitation is 62 cm (9/1978–9/2005 Normals, Western Regional Climate Center, Old Faithful). Average total snowfall is 540 cm, with an average depth of 33 cm. Average monthly maximum temperature is 9.6°C (−2.0°C in January and 23.6°C in July) and average monthly minimum temperature is −7.4°C (−17.8°C in January and 3.9°C in July). Soils in YNP are derived from relatively infertile rhyolitic substrates, intermixed with small areas of more mesic, and fertile soils derived from andesitic substrates and lacustrine sediments.

Study Design

In total, 77 sites that originated from stand-replacing wildfire were selected to span the range in age and density present across the park. To ensure, stands were equally sampled across the range of stand ages and densities, stands were initially grouped by age class (<20, 40–70, 80–130, 170–230, >250 years) and tree density class (low, moderate, or high density for stands <170 years). Stand age was determined by a combination of stand age maps (Romme and Despain 1989) and coring at least 8–10 dominant trees per stand. Stand age ranged from 12 to 331 years (median = 131 years). Tree density ranged from 425 to 598,462 stems ha^{−1} (median = 1325 trees ha^{−1}) (Supplementary Appendix 1). Total stem density (trees + saplings (<4 cm dbh)) averaged 45,523 (range = 850–1,202,462), with most variation in stem density occurring among young stands regenerating from the 1988 fire (Figure 1). Because the effects of serotiny on post-fire density are minimal beyond more than 170 years, mature stands were selected a priori by presence or absence of beetle-kill in the 1970s and 1980s. In

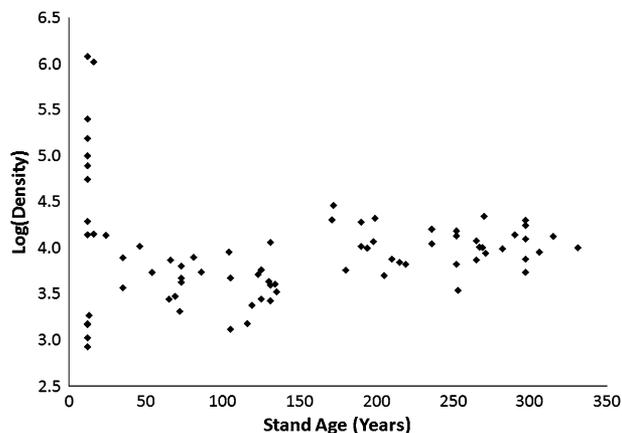


Figure 1. Stand age versus lodgepole pine density (stems ha^{−1}, including saplings (<4 cm) and trees (>4 cm)) among the sampled stands ($n = 77$) in the Greater Yellowstone Ecosystem.

these stands mountain pine beetles killed 20–70% of the dominant canopy trees (Romme and others 1986) but increased density of understory lodgepole. At the time of sampling, average tree density was 1,324 and 1,066 trees ha^{−1} in beetle and non-beetle stands, respectively (Supplementary Appendix 1) and total density including saplings (<4 cm dbh) was 12,256 for beetle stands and 11,922 for non-beetle stands. At each site, 3 plots (10 × 50 m) were established, separated by approximately 50 m, for a total sample area per stand of 6,500 m². Local disturbance histories are difficult to determine, and these stands may have experienced different levels of insect attacks, canopy gaps, and low-intensity surface fires during the interval between stand-replacing fires.

N stocks and Litterfall N flux

Allometric calculations to calculate aboveground mass for *P. contorta* in the GYE were developed by Arcano (2005) and C data for each stand will be reported elsewhere (Kashian and others, unpublished). Coarse root and aboveground tree biomass was adjusted using double sampling based on detailed measurements of 30 trees (Cochran 1977). Standing dead N stocks were estimated using allometric equations in Pearson and others (1984). Aboveground biomass, litterfall and forest floor data for the 12 stands less than 20 years old were taken from Litton and others (2004), but coarse woody debris (CWD) was resampled. In all stands, CWD was sampled using the line (planar) intercept method along 2,450-ft transects (1,200 ft per

transect) (Brown 1974). Forest floor N was collected within a 30 cm² square frame, down to mineral soil. Mineral soil was collected immediately below the forest floor sample using a soil tube (6.35 cm diameter vs. 30 cm long). Live fine root N from the top 15 cm of mineral soil was taken from Litton and others (2004) if available (Supplementary Appendix 1). Otherwise, fine root N concentration was measured in mineral soil at two depths (0–15 and 15–30 cm) for each plot. Fine roots were limited to mineral soil rather than forest floor in most stands. Rare exceptions were stands with larger understory sedge communities, in which case small root N would be included in the overlying forest floor N pool. Forest floor and soil N concentrations were based on plot composites ($n = 3$ composites per stand, one from each plot, comprised five samples per plot). Soil N and bulk density (fine fraction, <2 mm) were also composited separately at each depth (0–15 and 15–30 cm). Litterfall was collected in 4 litter traps per plot ($n = 12$ per stand, each trap was 0.142 m²). Traps were left out for 1 year (June 2004–June 2005), emptied, and then left out again for a second year (June 2005–June 2006). Fine root, litterfall, and forest floor stocks were corrected using ash-free dry weights. We expect leaching losses from collected litter were significant in winter and spring. On the other hand, Remsburg and Turner (2006) found substantial immobilization of N into needle and herbaceous litter following 2 years of litter bag incubations in situ in YNP. Thus, our annual litterfall N measures reflect net N concentrations that may integrate leaching loss and immobilization gains and do not represent N concentrations of recent litterfall material.

Total N stocks were calculated for each pool by multiplying mass by N concentration. N concentrations were either taken from the literature (aboveground wood, decay class 1–2 coarse downed wood larger 3 cm dbh, and standing dead wood) or analyzed in this study (decay class 3–5 downed wood, fine roots, forest floor, soil N). Live wood N concentration was assumed to be 0.03% (Fahey and others 1985; Pearson and others 1987). Decay classes 1 and 2 downed wood N concentration and standing dead wood N concentration (% dry mass) were taken from Fahey (1983) as 0.065 (class 1) and 0.103 (class 2), and 0.04 (standing dead wood). To calculate N concentrations for the other pools, subsamples were ground to pass through a 0.5-mm² mesh (size 40) and then analyzed for total N concentration on a LECO-100 CHN analyzer at Colorado State University (LECO Corporation, St. Joseph, MI, USA). Downed wood

N (% dry mass) for classes 3, 4, and 5 coarse wood were 0.273, 0.323, and 0.314%, respectively. Stump mass was converted to N using the average N content of all five CWD classes (0.216%). Composite foliar N concentrations were 1.2% for saplings (<20 years) and 0.87% for trees (>35 years).

Soil N Availability

Annual soil N availability was measured using in situ ion-exchange free resin bags buried in the soil (Binkley and Matson 1983; Binkley and others 1992) at 58 sites. In addition, previously published resin bag data (Litton and others 2004) was available for another 12 stands for a total of 70 stands. Ion exchange resins provide a relative measure of soil N availability by adsorbing N in soil solution to the resin surfaces. Resin bags are correlated with the more labor-intensive estimates of inorganic N mineralization derived from resin cores (Binkley and Matson 1983) and are effective for indexing N availability across remote settings (Litton and others 2004). Resin bags were assembled of nylon stocking material and contained 20 g of cation/anion exchange resin beads (J.T. Baker #4631) and were pre-rinsed in 2 M KCl. Resin bags were placed slightly underneath the mineral soil layer (enough to prevent exposure) in July 2004 and removed in July 2005, and exact incubation days were recorded. Five resin bags were randomly placed surrounding a center stake at each of the three plots per stand ($n = 15$ bags per stand). After collection, resin bags were refrigerated and shipped to the University of Wisconsin—Madison for laboratory analysis. Due to time limitations, resin bags were not re-installed in the 12 sites sampled by Litton and others (2004) and data from these 12 sites are included along with 3 new sites in the less than 20-year age class. Average available N in the new stands was higher but more variable than in the stands sampled previously ($0.90 \pm 0.40 \mu\text{N bag}^{-1} \text{d}^{-1}$ (mean ± 1 standard error), $n = 3$, vs. $0.57 \pm 0.07 \mu\text{N bag}^{-1} \text{d}^{-1}$, $n = 12$) and was not statistically different ($P < 0.05$).

Resin bags were rinsed with DI water to remove soil adhered to the outside of the bag, and then air-dried. Bags were extracted in 75 ml of 2 M KCl and filtered (0.7 μm , sample-rinsed filter paper). Each of the five individual resin bags per plot plus a composite sample per plot was extracted. Plot composites were analyzed colorimetrically for NH_4^+ -N and NO_3^- -N using a flow-injected autoanalyzer at the University of Wyoming (Technicon TrAAcs 800, Technicon Corporation). If a composite sample exceeded a reasonable range compared to the other

values in the dataset ($>10 \mu\text{g bag}^{-1}$), the original five individual samples from the plot were analyzed to ensure the composite sample was representative.

General Soils

A composite soil sample from each stand was analyzed for general soils characteristics (Midwest Laboratories, Omaha, NE) at both 0–15 cm and 15–30 cm soil depths. Variables analyzed included percent organic matter, weak Bray P (extraction with dilute acid and ammonium fluoride), strong Bray P (extraction with four times the acid concentration), as well as potassium (K), magnesium (Mg), and calcium (Ca) (extraction with a Mehlich-3 solution in a 1:10 (soil:extractant) ratio and analyzed by atomic adsorption). Cation exchange capacity (CEC) was measured by summing the exchangeable bases and exchangeable acidity (pH, measured with 0.1 M CaCl_2). All methods followed recommended soil test procedures for the North Central region, USA (NCR 1998).

Calculations and Statistics

Model selection to predict resin-sorbed N and ecosystem N pools and soil characteristics, across all stand ages and densities, was computed in SAS (version 9.1, SAS Institute, Cary, NC) to determine the top 15, 3-variable, candidate models, followed by calculation of Akaike information criterion (AIC_c). The full model included only terms that were not significantly correlated to each other based on Pearson correlation coefficients ($P > 0.05$). Models that had Δi less than 2, and for which

ω_i was within 10% of the top model were assumed to be the best model given the data. All data were checked for normality; soil N availability and tree density were log transformed prior to analyses. Relative nitrification was calculated as NO_3^- divided by total $\text{NH}_4^+ + \text{NO}_3^-$. Forest floor residence time (years) was calculated as forest floor N mass divided by annual litterfall N. This variable is only a relative index of among-stand variation because it is based on assumptions of steady-state conditions. All calculations and statistical analyses used stand as the experimental unit and used a significance level of $\alpha = 0.05$.

RESULTS

Effects of Stand Age and Tree Density on Resin-Sorbed N

Resin-sorbed N ($\text{NH}_4^+ + \text{NO}_3^-$) ranged from 0.07 to $3.20 \mu\text{N bag}^{-1} \text{d}^{-1}$ among stands, averaging $0.97 \pm 0.09 \mu\text{N bag}^{-1} \text{d}^{-1}$ (mean ± 1 standard error). Resin-sorbed NO_3^- ranged from 0.01 to $3.00 \mu\text{N bag}^{-1} \text{d}^{-1}$ among stands, averaging $0.67 \pm 0.07 \mu\text{N bag}^{-1} \text{d}^{-1}$. On average, NO_3^- accounted for $65 \pm 3\%$ of total resin-sorbed N. Resin-sorbed NH_4^+ ranged from 0.03 to $1.32 \mu\text{N bag}^{-1} \text{d}^{-1}$ among stands, averaging $0.32 \pm 0.03 \mu\text{N bag}^{-1} \text{d}^{-1}$.

Together, age and density and their interaction explained 19% of the variation in resin $\text{NH}_4^+ + \text{NO}_3^-$ and 22% of the variation in resin-sorbed NO_3^- , although stand density and the interaction term contributed little to the final model (Table 1). Across all stands, resin-sorbed NH_4^+ was not significantly related to stand age or density (Table 1). Both resin-sorbed NO_3^- and NH_4^+ tended to increase

Table 1. ANOVA Results Exploring Variation of Resin Bag N or Ecosystem N Pools Accounted for by Stand Age, Stem Density (Log Transformed, Saplings + Trees), or Their Interaction Among 77 Chronosequence Stands in the Greater Yellowstone Ecosystem

	Age	Density	Age \times density	Full model		
				R^2	<i>F</i>	<i>P</i>
Resin NH_4^+				Ns		
Resin NO_3^-	0.13**	0.05*	Ns	0.22	5.89	**
Resin $\text{NH}_4^+ + \text{NO}_3^-$	0.12**	Ns	Ns	0.19	4.74	**
Live N	0.31***	Ns	Ns	0.35	12.95	***
Detrital N	0.17**	Ns	Ns	0.18	5.36	**
Soil N	0.12**	Ns	Ns	0.14	3.81	*
Total N				Ns		

*** $P < 0.001$

** $P < 0.005$

* $P < 0.05$

Ns not significant

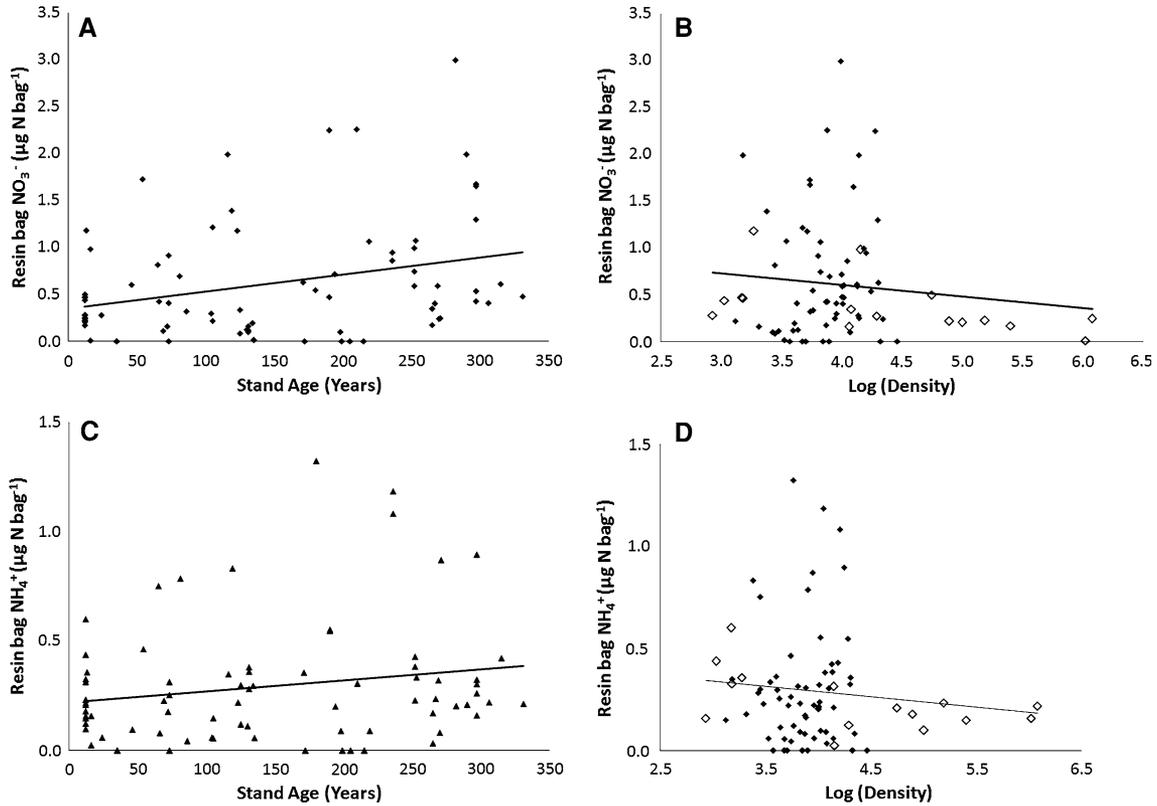


Figure 2. Relationship between resin-sorbed nitrogen and stand age and stem density in the Greater Yellowstone Ecosystem: **A** resin-sorbed nitrate (NO_3^-) versus stand age, **B** resin-sorbed NO_3^- versus stem density, **C** resin-sorbed ammonium (NH_4^+) versus stand age, **D** resin-sorbed NH_4^+ versus stem density. For density figures, *trendline* represents best fit across all stands; *closed symbols* = stands older than 20 years; *open symbols* = stands younger than 20 years.

with stand age and decrease with density but there was substantial site variation (Figure 2). For both NH_4^+ and NO_3^- , young (<20 years old) stands with high densities governed this relationship, whereas older stands appeared to show no clear relationship between resin N and stem density. Among young stands (<20 years), total resin bag N was negatively related to stem density ($\text{adj } R^2 = 0.47$, $P = 0.003$, Figure 3).

Model selection based on AIC_c resulted in several competitive models for predicting resin bag N (Table 2). Age, total soil N, Ca_{0-15} , and P_{0-15} were included in the top candidate model for resin-sorbed NH_4^+ ($\text{adj } R^2 = 0.18$). Ca_{0-15} , P_{0-15} , and bulk density were included in the top model for resin-sorbed NO_3^- ($\text{adj } R^2 = 0.25$); other variables in competitive models for NO_3^- included stem density, pH, and litterfall N. Litterfall N and pH_{0-15} were included in the top model for total resin-sorbed N ($\text{adj } R^2 = 0.27$); other variables in competitive models included stand age, P_{0-15} , and bulk density. Total resin N was negatively correlated with soil pH_{0-15} (Figure 4). Most models to predict relative

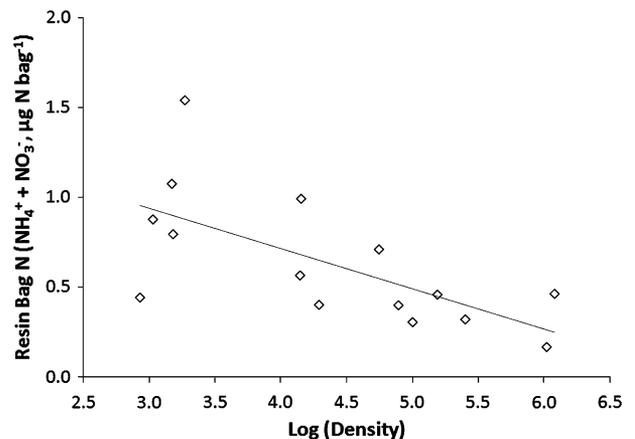


Figure 3. Total resin-sorbed N ($\text{NH}_4^+ + \text{NO}_3^-$) versus stem density among young stands younger than 20 years.

nitrification included P and bulk density, and occasionally soil N, total N, pH, or tree density (top candidate model $\text{adj } R^2 = 0.21$).

Table 2. Best Three Variable Candidate Models to Predict Resin-Sorbed Nitrogen Among Chronosequence Stands in the Greater Yellowstone Ecosystem

	K	Adj R^2	R^2	Variables	Δi	ωi
Resin NH_4^+	5	0.18	0.22	(+)Age, (+)soil N, (-)Ca ₀₋₁₅	0	0.16
	5	0.17	0.21	(+)Age, (+)soil N, (-)P ₀₋₁₅	0.75	0.11
	4	0.14	0.17	(+)Age, (+)soil N	0.88	0.10
	5	0.16	0.20	(+)Age, (-)total N, (-)Ca ₀₋₁₅	0.93	0.10
	4	0.14	0.17	(-)Total N, (-)Ca ₀₋₁₅	0.96	0.10
Resin NO_3^-	5	0.25	0.29	(-)Ca ₀₋₁₅ , (-)P ₀₋₁₅ , (-)bulk density	0	0.14
	5	0.25	0.29	(-)density, (-)pH ₀₋₁₅ , (-)P ₀₋₁₅	0.23	0.13
	5	0.25	0.29	(-)litter N, (-)pH ₀₋₁₅ , (-)P ₀₋₁₅	0.34	0.12
	5	0.24	0.28	(-)litter N, (-)Ca ₀₋₁₅ , (-)bulk density	0.75	0.10
	5	0.24	0.28	(-)density, (-)P ₀₋₁₅ , (-)bulk density	0.99	0.09
	5	0.23	0.27	(-)litter N, (-)pH ₀₋₁₅ , (-)bulk density	1.79	0.06
	4	0.20	0.23	(-)pH ₀₋₁₅ , (-)P ₀₋₁₅	1.98	0.05
Resin $\text{NH}_4^+ + \text{NO}_3^-$	5	0.30	0.33	(-)litter N, (-)pH ₀₋₁₅ , (-)bulk density	0.55	0.15
	4	0.27	0.30	(-)litter N, (-)pH ₀₋₁₅	0.91	0.13
	5	0.29	0.32	(+)Age, (-)litter N, (-)pH ₀₋₁₅		
Relative NO_3^-	4	0.21	0.24	(-)P ₀₋₁₅ , (-)bulk density	0	0.16
	5	0.22	0.26	(-)Soil N, (-)P ₀₋₁₅ , (-)bulk density	0.94	0.10
	5	0.22	0.26	(-)Total N, (-)P ₀₋₁₅ , (-)bulk density	0.98	0.10
	4	0.19	0.21	(-)pH ₀₋₁₅ , (-)P ₀₋₁₅	1.41	0.08
	5	0.21	0.25	(-)density, (-)P ₀₋₁₅ , (-)bulk density	1.68	0.07
	5	0.21	0.25	(-)Soil N, (-)pH ₀₋₁₅ , (-)P ₀₋₁₅	1.70	0.07

The top five candidate models were selected based on Akaike Information Criterion (AIC_c). A bias correction term was used to account for bias. Akaike weights, ω_i , were calculated as $e^{(-0.5*\Delta i)}/\sum e^{(-0.5*\Delta i)}$. Only models where Δi (AIC_c - min AIC) were less than 2 are shown. Sign of the effect of each variable in the full model is in parentheses.

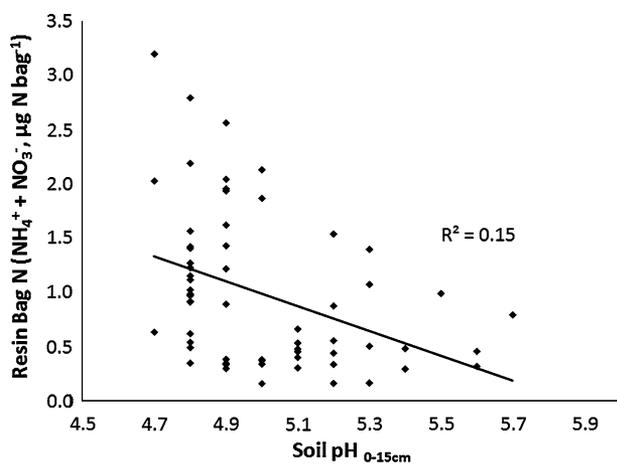


Figure 4. Total resin-sorbed N ($\text{NH}_4^+ + \text{NO}_3^-$) versus soil pH (0–15 cm) among all stands.

Effects of Stand Age and Tree Density on N Stocks

Total ecosystem N ranged from 63.7 to 185.8 g N m^{-2} across the chronosequence, averaging $109.9 \pm 3.0 \text{ g N m}^{-2}$ (Figure 5A). Total ecosystem N did not vary significantly with stand age or stand density (Table 1, Figure 5B).

Live N stocks (aboveground tree + sapling + coarse root + fine root_{0-30 cm}) were on average 14% of total ecosystem N. Live N averaged $14.8 \pm 0.8 \text{ g N m}^{-2}$ and ranged from 0.17 to 31.42 g N m^{-2} across the chronosequence. Live N increased with stand age (partial $R^2 = 0.31$) (Table 1, Figure 5A). As a percent of total ecosystem N, live N stocks increased with stand age, with most increases occurring less than 100 years (Figure 6). The largest fraction of live N was in aboveground tree N (bole + branches + foliage), which averaged $8.7 \pm 0.5 \text{ g N m}^{-2}$ across the chronosequence, followed by coarse root N, which averaged $5.1 \pm 0.2 \text{ g N m}^{-2}$ (Table 3). Fine root N was highest in the top 0–15 cm of soil ($1.52 \pm 0.1 \text{ g N m}^{-2}$) compared to 15–30 cm ($0.62 \pm 0.1 \text{ g N m}^{-2}$). The amount of live N contributed by saplings ranged from 0 to 14.6 (0–96%) with the greatest contributions from young post-fire stands.

Detrital N stocks (downed and standing dead wood, stumps, dead fine roots_{0-30 cm}, and forest floor) averaged 29% of total ecosystem N. As with live N, detrital N stocks increased with stand age (Table 1; Figure 5A) and contributed an increasing proportion of total ecosystem N in older stands (Figure 6). Detrital N averaged $32.2 \pm 1.5 \text{ g N m}^{-2}$ among stands and ranged from 10.1 to 79.0 g N m^{-2} .

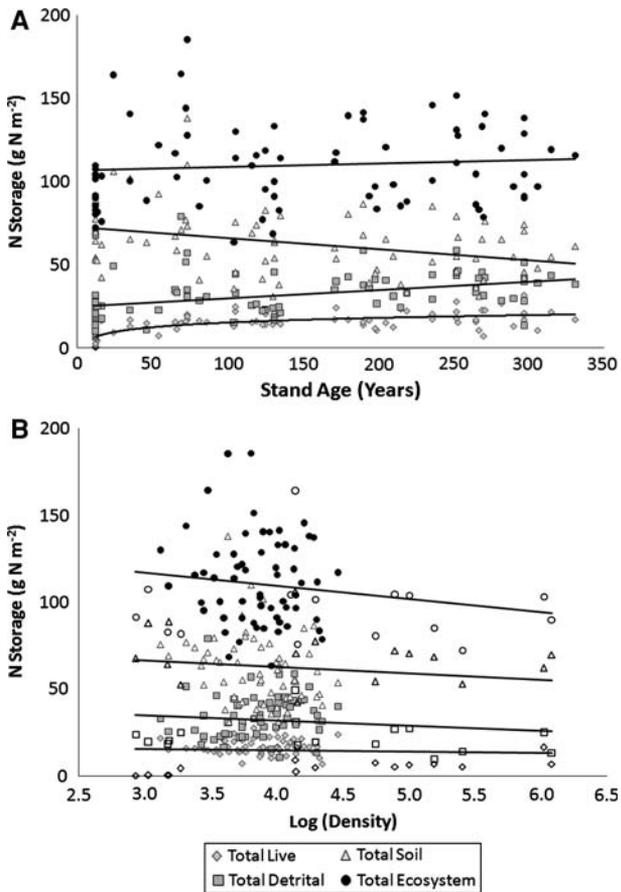


Figure 5. Live, detrital, soil, and total ecosystem nitrogen (g N m^{-2}) versus **A** stand age and **B** log (density) (closed symbols = stands >20 years; open symbols = stands <20 years).

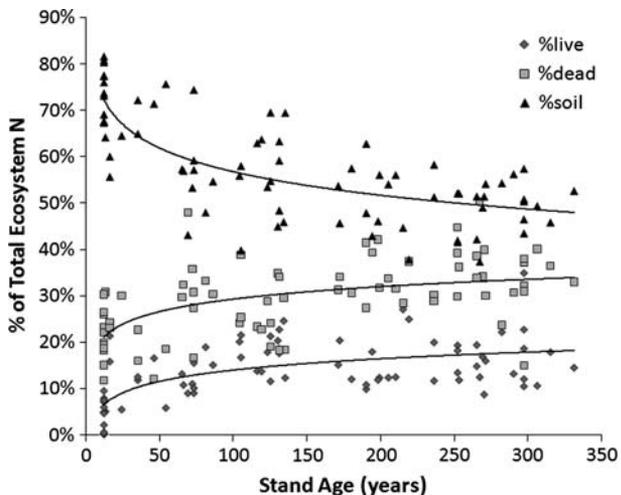


Figure 6. Percent of total ecosystem N accounted for by live, detrital, and soil N pools.

Forest floor N comprised the greatest proportion of detrital N ($15.3 \pm 1.0 \text{ g N m}^{-2}$) followed by downed wood N ($11.6 \pm 0.9 \text{ g N m}^{-2}$) (Table 3). Dead fine

roots comprised the least ($0.4 \pm 0.0 \text{ g N m}^{-2}$ at 0–15 cm and $0.1 \pm 0.0 \text{ g N m}^{-2}$ at 15–30 cm).

Soil N averaged $63.0 \pm 2.2 \text{ g N m}^{-2}$ and ranged from 30.9 to 138.1 g N m^{-2} among stands. Soil N stocks (0–30 cm) were 57% of total ecosystem N. Soil N decreased with stand age (partial $R^2 = 0.12$, full model $R^2 = 0.14$, $P < 0.05$, Table 1, Figure 5A), and represented a smaller portion of total ecosystem N in older stands (Figure 6).

Litterfall N ranged from 0.02 to $1.6 \text{ g N m}^{-2} \text{ y}^{-1}$ and averaged $0.6 \pm 0.0 \text{ g N m}^{-2}$. Forest floor residence times (forest floor mass/litterfall) ranged from 1.8 to 58.0 years and averaged 26.6 ± 1.6 years. Both litterfall N and forest floor residence time increased non-linearly with stand age, but did not vary with density (Figure 7). However, among stands less than 20 years old, litterfall N loads increased with stand density (adj $R^2 = 0.86$, $P < 0.001$ see dotted trendline in Figure 7B).

Statistical models to predict N stocks included stand age and variables describing soil chemistry. In addition, stem density was included in the top model to predict live N stocks in addition to pH_{0-15} , and bulk density (maximum adj $R^2 = 0.53$, Table 4). Models to predict detrital N included age, litterfall N, P_{0-15} , litterfall N, and bulk density (maximum adj $R^2 = 0.34$). Soil N stocks were best predicted by models that included stand age and resin-sorbed NH_4^+ (adj $R^2 = 0.18$). Models to predict total ecosystem N stocks included resin-sorbed NH_4^+ , pH_{0-15} , and Ca_{0-15} (adj $R^2 = 0.28$).

Effects of Stand Age and Tree Density on General Soil Characteristics

Results from the soil chemical analyses are reported in Table 5. Few soil characteristics were related significantly to stand age or density. K_{0-15} , pH_{0-15} , and bulk density were related significantly to density but explained little variation among stands (adj $R^2 = 0.12$, 0.07, and 0.06, respectively, data not shown). Similarly, K_{0-15} , pH_{0-15} , and bulk density decreased with stand age (Figure 8A–C). Percent organic matter was lowest among intermediate aged stands and higher among younger and older stands (Figure 8D). There was no significant relationship between Ca (Figure 8E), P (Figure 8F), Mg, or CEC with stand age or density at any depth measured.

DISCUSSION

Where appropriate, chronosequence studies are useful for substituting space for time allowing for

Table 3. Mean (± 1 Standard Error) Total Ecosystem N Stocks (g N m^{-2}) and Coefficient of Variation (%) Among 77 Chronosequence Stands in the Greater Yellowstone Ecosystem

		Mean ± 1 standard error	Coefficient of variation (%)
Live N	Aboveground tree	8.68 \pm 0.46	41
	Sapling	1.69 \pm 0.30	155
	Coarse root	5.06 \pm 0.23	36
	Fine root _{0-15cm}	1.52 \pm 0.13	73
	Fine root _{15-30cm}	0.62 \pm 0.06	79
Detrital N	Downed wood	11.60 \pm 0.85	64
	Standing dead	2.25 \pm 0.26	103
	Stump	2.64 \pm 0.17	56
	Fine root _{0-15cm}	0.35 \pm 0.04	90
	Fine root _{15-30cm}	0.14 \pm 0.01	82
Soil N	Forest floor	15.28 \pm 0.97	56
	Soil _{0-30cm}	62.98 \pm 2.22	31

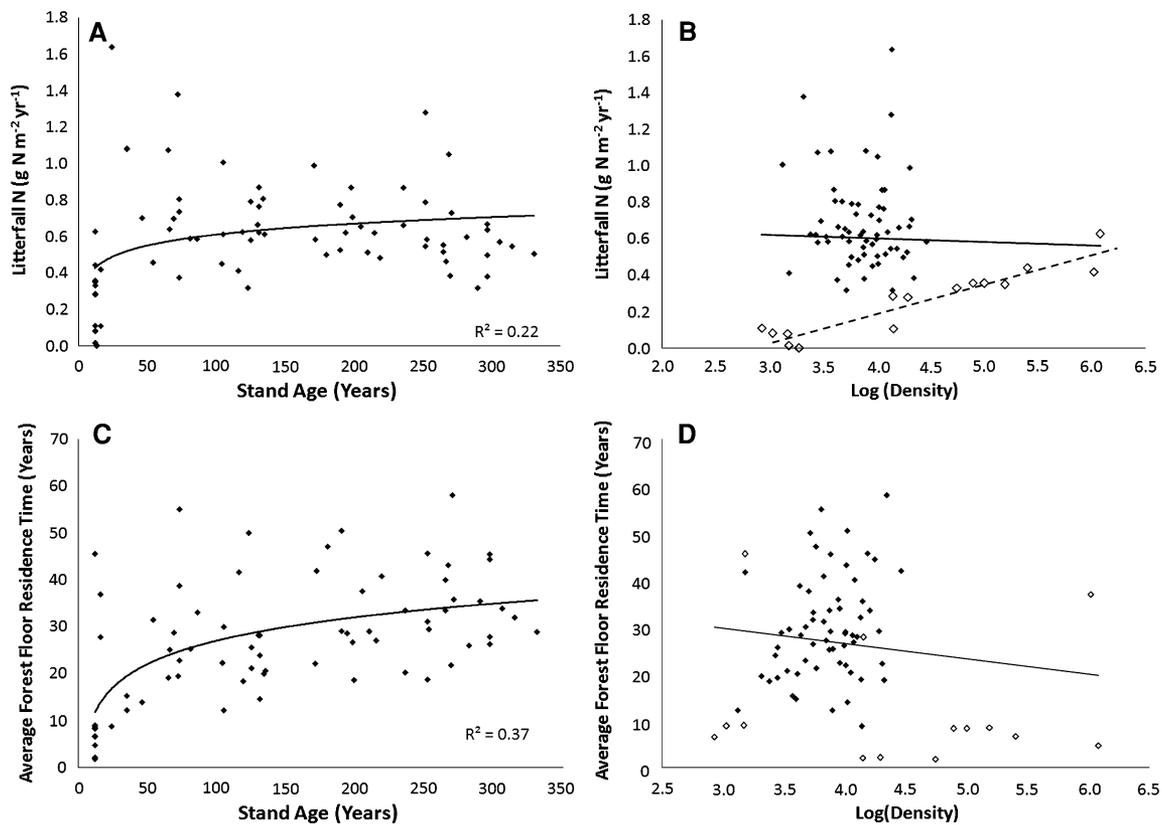


Figure 7. Relationship between litterfall N (g N m^{-2}) and forest floor residence times (years) with stand age (years) and density (stems ha^{-1}); *closed symbols* = stands older than 20 years; *open symbols* = stands younger than 20 years. **A** litterfall N versus stand age (years), **B** litterfall N versus density (stems ha^{-1}), **C** forest floor residence time (years) versus stand age, **D** forest floor residence times versus density. *Dotted line* in **B** represents trendline among stands younger than 20 years.

the ability to test for patterns of long-term ecosystem development but are notoriously difficult to constrain given variation in substrate, species, and disturbance histories. Here, we provide a replicated chronosequence study of 77 stands that are representative of post-fire successional trajectories and

stand conditions in a complex landscape in the Rocky Mountain West. The stands we studied were underlain by a single geologic substrate (rhyolite) and were dominated by a single species (lodgepole pine) that experience stand-replacing fire, allowing us to test for broad-scale variation in stand struc-

Table 4. Best Three Variable Candidate Models to Predict Ecosystem N Pools Among 77 Chronosequence Stands in the Greater Yellowstone Ecosystem

	K	Adj R ²	R ²	Variables	Δi	oi
Live N	5	0.53	0.55	(+)Density, (-)pH ₀₋₁₅ , (-)bulk density	0	0.20
	5	0.52	0.54	(+)Age, (+)pH ₀₋₁₅ , (-)bulk density	0.68	0.14
	5	0.51	0.54	(+)Age, (+)P ₀₋₁₅ , (-)bulk density	1.47	0.10
	5	0.51	0.54	(+)Age, (+)litterfall N, (-)bulk density	1.48	0.09
Detrital N	5	0.34	0.38	(+)Age, (+)P ₀₋₁₅ , (+)litterfall N	0	0.17
	5	0.34	0.37	(+)P ₀₋₁₅ , (+)litterfall N, (-)bulk density	0.47	0.13
	4	0.32	0.34	(+)P ₀₋₁₅ , (-)bulk density	0.60	0.13
	5	0.34	0.37	(+)Age, (+)P ₀₋₁₅ , (-)bulk density	0.66	0.12
	5	0.33	0.36	(+)Ca ₀₋₁₅ , (+)P ₀₋₁₅ , (-)bulk density	1.51	0.08
Soil N	4	0.18	0.21	(-)Age, (+)NH ₄ ⁺	0	0.20
	5	0.20	0.24	(-)Age, (+)NH ₄ ⁺ , (-)pH ₀₋₁₅	0.14	0.19
	5	0.19	0.23	(-)Age, (+)NH ₄ ⁺ , (+)litterfall N	1.02	0.12
	5	0.19	0.23	(-)Age, (+)NH ₄ ⁺ , (+)Ca ₀₋₁₅	1.08	0.12
	5	0.18	0.22	(-)Age, (+)NH ₄ ⁺ , (-)bulk density	1.37	0.08
Total N	5	0.28	0.32	(+)NH ₄ ⁺ , (-)pH ₀₋₁₅ , (+)Ca ₀₋₁₅	0	0.26

The candidate models were selected based on Akaike Information Criterion (AIC). A bias correction term was used to account for bias. Akaike weights, *oi*, were calculated as $e(-0.5*\Delta i)/\Sigma e(-0.5*\Delta r)$. Only models where Δi ($AIC_i - \min AIC$) were less than 2 are shown. Sign of the effect of each variable in the full model is in parentheses.

Table 5. Mean Values (±1 Standard Error) and Coefficients of Variation for General Soil Properties (Phosphorus (P), Potassium (K), Magnesium (Mg), Calcium (Ca), pH, Percent Organic Matter (OM), Cation Exchange Capacity (CEC), and Bulk Density) Among 77 Chronosequence Stands in the Greater Yellowstone Ecosystem

Soil variable	Mean ± 1 standard error	Coefficient of variation (%)
Weak P _{0-15cm} (kg ha ⁻¹)	57 ± 6	81
Weak P _{15-30cm} (kg ha ⁻¹)	60 ± 6	81
Strong P _{0-15cm} (kg ha ⁻¹)	118 ± 9	61
Strong P _{15-30cm} (kg ha ⁻¹)	117 ± 9	63
K _{0-15cm} (kg ha ⁻¹)	257 ± 6	19
K _{15-30cm} (kg ha ⁻¹)	222 ± 6	20
Mg _{0-15cm} (kg ha ⁻¹)	157 ± 6	31
Mg _{15-30cm} (kg ha ⁻¹)	154 ± 7	33
Ca _{0-15cm} (kg ha ⁻¹)	1023 ± 38	31
Ca _{15-30cm} (kg ha ⁻¹)	987 ± 39	31
pH _{0-15cm}	5.01 ± 0.0	5
pH _{15-30cm}	5.17 ± 0.0	3
%OM _{0-15cm}	2.6 ± 0.1	23
%OM _{15-30cm}	1.4 ± 0.1	34
CEC _{0-15cm}	5.6 ± 0.2	23
CEC _{15-30cm}	4.7 ± 0.2	28
Bulk density	0.83 ± 0.0	17

ture and age, independent of substrate and species differences. Stand age, density, and soil characteristics were the focus of our study design, and we

were not able to account for other factors such as fire severity (Turner and others 1997).

To our knowledge, this replicated chronosequence represents the most comprehensive assessment of N stocks and soil N availability with stand age in a temperate ecosystem. However, it is important to assess whether this level of analysis is necessary to uncover trends in ecosystem N storage across complex landscapes. To explore this, we randomly selected half our stands and reran our statistics on stand age and density. We found that explained variance and significance decreased for resin bag N when we included fewer stands (from $R^2 = 0.29$, $P < 0.0001$ to $R^2 = 0.20$, $P = 0.07$ for total resin N, and from $R^2 = 0.26$, $P = 0.0003$ to $R^2 = 0.17$, $P = 0.12$, for nitrate). This indicates improved statistical power for detecting patterns in N availability by including more stands. On the other hand, models improved slightly for predicting N stocks from stand age and density when we ran the statistics on half as many stands (vs. Table 1: live N $R^2 = 0.31$, $P = 0.005$; dead N $R^2 = 0.22$, $P = 0.04$; soil N $R^2 = 0.31$, $P = 0.005$; total ecosystem N $R^2 = 0.30$, $P = 0.006$). The fact that the models differed when including twice as many stands indicates the substantial among-stand complexity on the Yellowstone landscape that is included in our broader statistical analysis.

We were able to support the hypothesis that among younger stands (<20 years), soil N availability is lower among stands of higher stem density, supporting the earlier results of Litton and

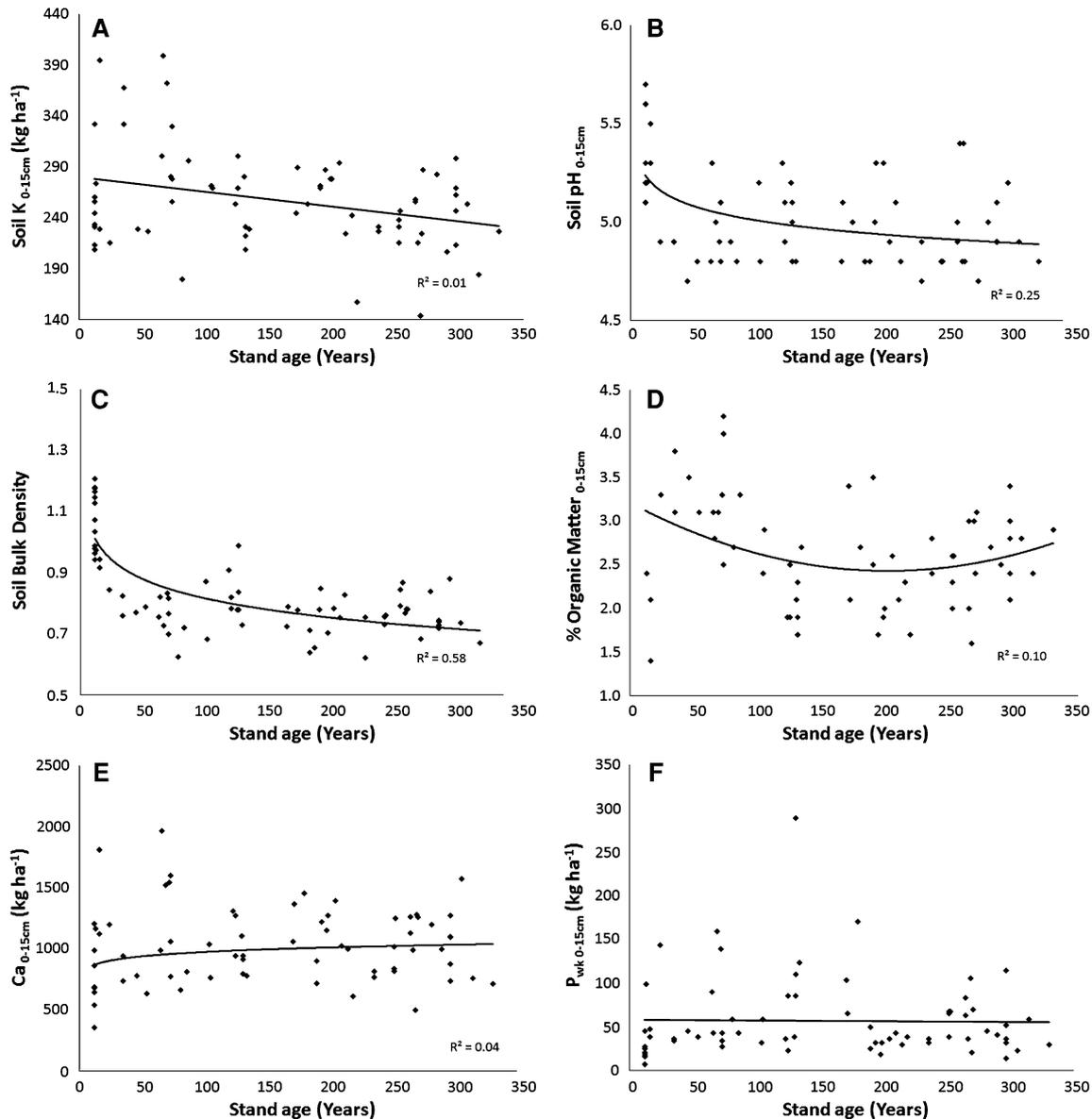


Figure 8. Soil characteristics in top 0–15 cm versus stand age. **A** K, **B** pH, **C** bulk density, **D** % organic matter, **E** Ca, **F** weak Bray P.

others (2004) and Levitt (2006). Moreover, the relationship between soil N availability and density across all stands is dominated by these density differences among young stands, with no clear density relationship among stands older than 20 years. In general, N availability increased with stand age, but regression models indicated that other variables, especially calcium and phosphorus concentrations, pH, and bulk density were also important.

There is conflicting evidence about trends in N availability with stand age. Other studies have indicated complex trends in post-fire soil N availability. Fire is known to increase short-term

(<5 years) soil N availability (Wan and others 2001; Smithwick and others 2005; Turner and others 2007) and may result in the relative conservation of N relative to C, depending on local factors including pre-fire fuel loads and stoichiometry and the fire-mediated redistribution of N (Harden and others 2002). However, these increases are often followed by a decline in soil N availability (Marion and Black 1988; Carreira and others 1994). In a jack pine (*P. banksiana*) forest in Michigan (USA), N mineralization rates were highest immediately following fire, decreased to low levels by 14 years and increased again through

70 years, which was attributed to increasing stocks of soil organic matter (Yermakov and Rothstein 2006). Studies that have shown equivocal or non-significant trends in N availability (Maclean and Wein 1977; Fenn and others 1993) have attributed their results to variation in fire intensity and post-fire conditions. We found that resin-sorbed NO_3^- and total N ($\text{NH}_4^+ + \text{NO}_3^-$) were positively correlated with stand age, but including information on soil chemistry further improved models. Multivariate relationships were not strong, however, indicating that patterns remain complex across the Yellowstone landscape.

Soil pH, P, Ca, and bulk density were included in final models to predict N availability, suggesting that these local soil characteristics are important for determining available N in lodgepole pine stands in the GYE. Previous studies have indicated that pH governs net N mineralization and nitrification. Specifically, nitrification appears to be stimulated by increasing pH and may require pH values above a critical threshold (Ste-Marie and Paré 1999; Sahrawat 2008). In our study, pH values ranged from 4.7 to 5.7 (average = 5.01 ± 0.03) in the top 15 cm of soil and from 4.9 to 5.7 (average 5.2 ± 0.02) between 15 and 30 cm, spanning the critical threshold for nitrification (5.3) identified by Ste-Marie and Paré (1999) in post-wildfire forests. Nitrification appears to be curtailed at pH below 5 and rapid with pH above 6 (Sahrawat 2008). In our study, total resin N was negatively correlated with pH across the range of pH measured (4.7–5.7) (Figure 7). Relative nitrification was not significantly correlated with pH_{0-15} but models to predict relative nitrification consistently included soil P_{0-15} in addition to bulk density and ecosystem N pools.

Despite the patterns described above, our results can provide only a relative index of N availability and do not indicate actual plant-available N pools. For example, our sampling design may have not accurately represented rooting depth or the spatial variability in soil N pools. Moreover, trees may respond to availability of different N forms (for example, organic N, Neff and others 2003), which were not measured using resin bags. Organic N uptake has recently been shown to equal or exceed uptake of inorganic N sources in Scots pine (Persson and others 2006). Moreover, lodgepole pine trees are associated with ectomycorrhizal species (Douglas and others 2005), which have been shown to recolonize seedlings quickly following fire (Miller and others 1998). Further studies are needed to determine whether these ectomycorrhizal associations modify the relative patterns in inorganic and organic N uptake.

We also expected that N stocks would be recovered by 70–100 years following fire due to previous modeling results. Our chronosequence measurements confirm that live N stocks increase with stand age and increase dramatically as a proportion of total ecosystem N up to 100 years following fire. Detrital wood N (standing + downed), forest floor N, and litterfall N also increased with stand age, and most increases were within the first 50–100 years of stand development with no significant differences among older stands. In contrast, soil N decreased with stand age.

Total ecosystem N, which integrates patterns in live, detrital and soil N, was not related to stand age or density alone. Thus, although the relative proportion of N stocks vary with stand age, total ecosystem N is not affected over the long term by stand-replacing fire in these lodgepole pine forests. Because N combusts at relatively low temperatures (Knight 1966), N has the potential to be lost following fire (Raison 1979; Raison and others 1985). However, fire also converts organically bound N to inorganic forms and may increase inorganic N supply over the short term (Wan and others 2001), potentially alleviating N limitations in ecosystems experiencing infrequent fire. And, despite the relatively low combustion temperatures of N, the total amount of ecosystem N combusted appears to be small following wildfire, for example, less than 1 to 6% of total prefire N (Page-Dumroese and Jurgensen 2006). The low total combustion of N is partially due to the fact that most ecosystem N is stored in soil organic matter (Fahey 1983; Smithwick and others 2009) that is relatively unaffected by fire. In addition, coarse wood consumption was measured as less than 8% following the 1988 Yellowstone fires (Tinker and Knight 2000). In conjunction with the rapid recovery of lodgepole pine due to serotinous cones, N losses appear to be rapidly recovered following stand-replacing fire. It appears, therefore, that there are few reasons to expect long-term N loss following infrequent, severe stand-replacing fire in these lodgepole pine ecosystems.

Fire is predicted to increase in severity under climate change for these subalpine forests (Westering and others 2006). In other systems, increases in fire frequency raise concerns of long-term N losses whereby combustion losses from fire are not recovered during relatively shorter fire return intervals (Ojima and others 1994). Given that the historical fire return interval is between 100 and 300 years and that the N stocks were recovered less than 100 years, we conclude that fire return intervals would need to be significantly reduced to have a significant impact on ecosystem N. This is

similar to previous modeling results for the Yellowstone ecosystem in which maximum changes to total ecosystem N would be 6.8% among differences in fire return intervals (293 vs. 172 years) or stand densities (dense vs. sparse regeneration) (Smithwick and others 2009). Similarly, C stocks appear to be more sensitive to changes in post-fire life form (for example, conversion of forest to meadow) or post-fire tree density than moderate variations in stand age (Kashian and others 2006).

In conclusion, we show that total ecosystem N is recovered quickly following stand replacing fire. Patterns in total ecosystem N stocks and inorganic soil N availability were largely governed by stand age in addition to site variation in pH, P, and Ca. This suggests that replicated chronosequences are necessary to determine the magnitude and directionality of N dynamics on complex landscapes where soil biogeochemistry, stand structure and stand age differ. Given increases in fire frequency and severity under climate change for these subalpine forests, understanding the interactions between biogeochemistry, disturbances, and ecosystem productivity is critical. However, because we observed relatively few changes in total ecosystem N storage resulting from stand-replacing fire, we conclude that there will be a limited effect of altered fire regimes on ecosystem N storage over the long term in Greater Yellowstone.

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