Variation in foliar nitrogen and aboveground net primary production in young postfire lodgepole pine

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Abstract: Understanding nutrient dynamics of young postfire forests may yield important insights about how stands develop following stand-replacing wildfires. We studied 15-year-old lodgepole pine stands that regenerated naturally following the 1988 Yellowstone fires to address two questions: (1) How do foliar nitrogen (N) concentration and total foliar N vary with lodgepole pine density and aboveground net primary production? (2) Is foliar N related to litter production and to rates of gross production, consumption, and net production of soil NH_4^+ and NO_3^-? Foliar N concentration of new lodgepole pine needles averaged 1.38%; only stands at very high density (>80 000 trees·ha^{-1}) approached moderate N limitation. Foliar N concentration in composite (all-age) needles averaged 1.08%, varied among stands (0.87%–1.39%), and declined with increasing tree density. The foliar N pool averaged 48.3 kg N·ha^{-1}, varied among stands (3.6–218.4 kg N·ha^{-1}), and increased with aboveground net primary production. Total foliar N was not related to laboratory estimates of net production of NH_4^+ or NO_3^- in soils. Lodgepole pine foliage is a strong N sink, and N does not appear to be limiting at this early successional state. The initial spatial patterns of postfire tree density strongly influence landscape patterns of N storage.

Résumé : La compréhension de la dynamique des nutriments des jeunes forêts issues de feux peut fournir des renseignements importants sur le développement des peuplements à la suite d'un feu entraînant le remplacement des peuplements. Nous avons étudié des peuplements de pin tordu âgés de 15 ans qui se sont régénérés naturellement après les feux de 1988 dans le parc de Yellowstone pour répondre à deux questions : (1) comment la concentration d'azote (N) foliaire et le N foliaire total varient en fonction de la densité de pin tordu et de la production primaire nette aérienne (PPNA) ? (2) est-ce que le N foliaire est relié à la production de litière et aux taux de production brute, de consommation et de production nette de NH_4^+ et de NO_3^- du sol ? La concentration de N foliaire des nouvelles aiguilles de pin tordu était, en moyenne, de 1,38 %. Seuls les peuplements très denses (plus de 80 000 tiges·ha^{-1}) ont approché une limitation modérée en N. La concentration foliaire en N d'échantillons composites d'aiguilles de tous les âges était, en moyenne, de 1,08 %, variait de 0,87 % à 1,39 % parmi les peuplements et diminuait avec la densité du peuplement. Le réservoir de N foliaire était, en moyenne, de 48,3 kg N·ha^{-1}, variait de 3,6 à 218,4 kg N·ha^{-1} parmi les peuplements et augmentait avec la PPNA. Le N total foliaire n'était pas relié aux estimations faites en laboratoire de la production nette de NH_4^+ et de NO_3^- des sols. Le feuillage de pin tordu est un puits important de N qui ne semble pas être limitatif à ce jeune stade de succession. Les patrons spatiaux initiaux de la densité des peuplements issus de feux modifient les patrons d'entreposage de N à l'échelle du paysage.

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Introduction

Wildfire is a natural component of many forest ecosystems, and the frequency of large wildfires is increasing in the northern Rocky Mountains (Westerling et al. 2006) and North American boreal zone (Kasischke and Turetsky

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2006). Forest fires have received much attention in ecology, but the increased fire activity in subalpine and boreal forests underscores the need for a more complete understanding of the ecological consequences of large, severe fires. Because northern conifer forests are often thought to be nitrogen (N) limited (Vitousek and Howarth 1991), understanding postfire N cycling is increasingly important for understanding stand dynamics. N dynamics following low-severity fires have been well studied (e.g., Wan et al. 2001), but surprisingly little is known about changes in N following natural severe stand-replacing forest fires (Smithwick et al. 2005a). In this study, we report on variation in foliar N in 15-year-old lodgepole pine (*Pinus contorta* Dougl. ex Loud. var. *latifolia* Engelm. ex Wats) stands that established following the extensive 1988 fires in Yellowstone National Park, Wyoming, USA.

Foliar N is a useful indicator of forest N status because it is tightly linked to many ecosystem processes, including photosynthesis, net primary production (NPP), decomposition, and N mineralization (Ollinger et al. 2002). Landscape

variation in forest canopy N also serves as an effective integrator of factors that affect NPP. As forest succession proceeds following forest fire, plant N uptake increases, and the developing canopy assumes an increasingly important role in nutrient retention (Prescott 2002). Nutrient availability depends not only on soils and other site conditions but also on canopy characteristics, including foliar chemistry, because the canopy influences the amount and quality of leaf litter deposited on the forest floor (Prescott 2002). Therefore, understanding foliar N in the canopy may provide important insights into the N status of postfire forests.

Lodgepole pine is a dominant conifer in western forests from Colorado to the Yukon and typically grows in even-aged stands that establish after stand-replacing fire. Lodgepole pine uses N efficiently (Prescott et al. 1989), and N is often considered limiting to lodgepole pine growth (Fahey et al. 1985). However, N fertilization experiments have yielded conflicting results. Some fertilization studies have found strong evidence for N limitation (e.g., Weetman et al. 1988; Startsev et al. 2007), but others suggest that younger lodgepole pine stands may not be N limited (Brockley 2007; Romme et al. 2009). During fire, N is lost through combustion, and total ecosystem N may be reduced. Although such N losses could exacerbate potential N limitation, ecosystem N losses to fire may not be great (Page-Dumroese and Jurgensen 2006; Smithwick et al. 2008), and microbial immobilization can enhance N retention in the postfire ecosystem (Turner et al. 2007). Furthermore, soil inorganic N pools often increase after fire because of changes in detrital pools, soil temperature and moisture, and microbial activity (Smithwick et al. 2005a), so N supply could be adequate for tree growth during early succession. However, the variation in N pools and transformations in young forests developing after severe fire is not well known.

The foliar nutrition of lodgepole pine has been well studied in the context of forest management. Research has generated foliar nutrient diagnostic criteria for lodgepole pine based on current-year's foliage (Brockley 2001; Moore et al. 2004) and has provided important insights into the relative influence of different nutrients on lodgepole pine growth and foliar nutrition (e.g., Brockley 2007). Many studies have examined changes in nutrient accumulation rates and productivity with stand age in lodgepole pine (e.g., Pearson et al. 1987; Ryan et al. 1997), and some studies have considered tree density (e.g., Binkley et al. 1995; Blevins et al. 2005). However, few studies have examined variation in foliar chemistry among stands of naturally regenerated postfire lodgepole pine during the earliest phases of stand development (but see Litton et al. 2003, 2004).

The extensive 1988 fires in Yellowstone National Park produced a landscape mosaic of postfire lodgepole pine stands that vary widely in tree density (from 0 to > 500 000 trees·ha^{-1}) and aboveground net primary production (ANPP) (Turner et al. 2004). In this study, we sampled 14 postfire lodgepole stands spanning the observed range of tree densities to address two questions: (1) In 15-year-old postfire lodgepole pine stands, how do foliar N concentration and total foliar N vary with lodgepole pine density and ANPP? (2) Is foliar N concentration related to litter production and rates of gross production, consumption, and net production of soil NH_4^+ and NO_3^-?

We were also able to evaluate change in stand structure during this important phase of postfire succession because we had previous measurements (from 1999) of tree density and ANPP in these stands (Turner et al. 2004). We hypothesized that tree density could have declined in high-density stands resulting from density-dependent mortality, but we expected stand-level ANPP to have increased.

Although our study of foliar N is comparative and cannot conclusively identify N limitation in these young stands, results may provide insights about whether N is or is not likely to be limiting growth. Therefore, we framed our expectations as follows. We expected foliar N concentrations in new needles to be below the critical value (1.2%; Moore et al. 2004) if N was limiting. We also expected foliar N concentrations to decrease with increasing tree density if competition for N limited growth in these stands, as more trees would compete for a limiting resource. However, detecting such a relationship cannot alone identify N limitation; foliar N concentrations could either be unrelated to tree density (because N is readily available) or decrease with increasing tree density (because of a dilution effect) if N was not limiting (Binkley 1986). Thus, we further expected total foliar N (kg·ha^{-1}) to be unrelated to tree density if N was limiting (because the foliar N content would be constrained by available N) but to increase with tree density if N was not limiting (because more trees would be able to acquire more N). Finally, we expected to see a positive relationship between net N mineralization and ANPP, leaf area index (LAI), and total foliar N if inorganic N was limiting growth, and no relationship with ANPP, LAI, and foliar N if inorganic N was not limiting.

Methods

Study area

Our study was conducted in Yellowstone National Park (YNP), which encompasses approximately 9000 km^2 in Wyoming, USA. Approximately 80% of YNP is dominated by lodgepole pine forest, although subalpine fir (*Abies lasiocarpa* (Hook.) Nutt.), Engelmann spruce (*Picea engelmannii* Parry), and whitebark pine (*Pinus albicaulis* Engelm.) may be locally abundant in older stands at higher elevations or on moister sites. The climate is characterized by cold, snowy winters and dry, mild summers, with mean January temperature of –11.4 °C, mean July temperature of 10.8 °C, and mean annual precipitation of 56.25 cm (Dirks and Martner 1982). Large fires occur in YNP with a return interval of about 170–300 years (Schoennagel et al. 2003). Our study was conducted in the central and southern portions of YNP that experienced stand-replacing fires during 1988. All sites had minimal topographic relief and were dominated by lodgepole pine both before and after the 1988 fires.

Vegetation sampling

From 90 stands that were initially sampled in 1999 (Turner et al. 2004), we selected a subset of 14 stands (Table 1) that spanned the range of postfire lodgepole pine densities and ANPP observed in 1999 and were reasonably accessible (≤2 km from a road). All stands were located on infertile soils (shallow inceptisols) derived from rhyolite or tuff and were between 2000 and 2500 m elevation. Stands

Table 1. Location, tree density, soil pH, total organic matter (OM), and total nitrogen for 14 stands of postfire lodgepole pine.

Site name	Easting (UTM[a])	Northing (UTM[a])	2003 tree density (trees·ha⁻¹)	Soil pH	Soil OM[b] (%)	Soil total N[c] (%)	Soil C/N ratio[d]
Cascade Meadows North	537625	4953870	533	5.2	3.1	0.04	45.0
Lewis Canyon (actual)	527329	4896594	467	5.2	3.7	0.09	23.8
Pitchstone Hobo	528552	4900863	1 100	5.7	4.0	0.09	25.8
84 Blowdown	527888	4951568	3 700	5.5	2.0	0.04	29.0
Heart Lake Trail	534350	4906927	6 933	5.2	4.4	0.07	36.5
Cascade Meadows South	536876	4951792	9 000	5.3	2.7	0.05	31.3
Cygnet Lakes North	532022	4950292	10 333	5.3	3.6	0.07	29.8
Lewis Canyon Creighton	527200	4893800	11 667	na	na	na	na
Riddle West	535008	4912531	16 100	na	na	na	na
Riddle High	532151	4909604	26 367	5.1	3.4	0.07	28.2
Gibbon Falls	515479	4944380	43 633	5.6	2.0	0.05	23.2
Firehole Loop South	511433	4940967	61 633	5.6	1.6	0.03	30.9
Gravel Pit	500984	4945028	454 200	5.6	2.5	0.04	36.3
Fountain East	499486	4943962	535 000	5.7	3.4	0.07	28.2

Note: All stands were located in Yellowstone National Park, Wyoming, on infertile soils derived from Quaternary rhyolite or tuff, and all established after the extensive fires of 1988. na, not available.

[a]NAD 83, Zone 12N; UTM, Universal Transverse Mercator.

[b]Dry combustion using the Tekmar-Dohrman 183 TOC Boat Sampler DC-190 (Tekmar-Dohrman, Mason, Ohio).

[c]Micro-Kjeldahl procedure.

[d]Assuming a carbon-to-organic matter ratio of 0.58.

were relocated in the field in July 2003 by navigating from global positioning system coordinates and locating the permanent marker for the plot, and a 0.25 ha plot (50 m × 50 m) was laid out. Vegetation was sampled following the same protocols used in 1999 (see Turner et al. 2004). Briefly, postfire lodgepole pine density was recorded along three 50 m × 2 m belt transects in each plot; the basal diameter, height, and annual height increment of lodgepole pine saplings ($n = 25$) was recorded, and percent cover by species was recorded within 0.25 m² circular sampling frames along each of the three transects ($n = 25$ frames). All sampling was conducted between July and August 2003.

Lodgepole pine ANPP, LAI, and foliage biomass were estimated for each stand by using allometric relationships we developed previously in our study area for 10-year-old postfire saplings (Turner et al. 2004). We confirmed that these allometric equations were still appropriate for the 15-year-old trees by harvesting 86 trees of various sizes in 2003 and testing the predicted vs. observed ANPP and biomass. Regression analysis demonstrated that the predicted and measured values were well correlated ($r^2 = 0.96$ for both ANPP and foliage biomass; $P < 0.05$). Regression coefficients for ANPP (intercept = 4.7, 95% CI of –25.7–35.2; slope = 1.04, 95% CI of 1.0–1.08) and foliage biomass (intercept = 16.9, 95% CI of –16.6–50.5; slope = 1.10, 95% CI of 1.0–1.15) did not differ from a 1:1 relationship. Thus, ANPP for each of the 25 measured trees in each stand was estimated using the nonlinear allometric equation $Y = aX^b$, where X is the outside bark basal diameter (cm), $a = 9.539$, and $b = 2.577$ (Turner et al. 2004). These estimates were averaged to estimate a mean per tree annual ANPP rate (g·tree⁻¹) for each stand. Stand-level annual ANPP (Mg·ha⁻¹) was computed by multiplying the mean per tree ANPP estimate by tree density. We estimated the biomass of live *P. contorta* foliage similarly by applying our allometric equation ($Y =$

aX^b, where X is the outside bark basal diameter (cm), $a = 7.193$, and $b = 2.729$; Turner et al. 2004) to compute foliage biomass (g) for each measured tree, determining the average foliage biomass per tree for that stand, then multiplying the average by tree density. Herbaceous ANPP was computed using species-specific allometric equations based on percent cover and was developed in our study region (Turner et al. 2004). Our calculations do not account for losses to herbivory, but we observed no evidence of aboveground herbivory on lodgepole pine saplings and little to no herbivory on herbaceous vegetation.

Foliar nitrogen and carbon

Foliage was collected from nine lodgepole pine saplings in each stand by selecting the nearest tree at the 5, 25, and 45 m positions along each of the three transects. Three branches were harvested from each tree, one each from high, intermediate, and low canopy positions. Branches were placed in labeled paper bags and returned to the laboratory, where all needles were removed from each branch and dried to constant mass at 60 °C. In addition, we collected branches from which we removed only the new needles so that foliage of the year could be analyzed separately and compared with critical foliar levels indicative of N limitation (Brockley 2001). Foliage was kept dry, ground, and analyzed for percent N and carbon (C) on a LECO CHN dry-combustion analyzer (LECO, St. Joseph, Michigan). To compute total foliar N in each stand (kg N·ha⁻¹), we computed the mean percent foliar N from composite foliage samples (i.e., all needle ages), then multiplied that value by the foliage biomass for the stand.

Litter quantity

We deployed 16 litter traps in each stand during summer 2003 and retrieved them in summer 2004 to obtain an index

of litter production. Traps were plastic baskets (surface area 1200 cm^2 with 15 cm high sides to retain litter in the basket) in which we extended weed stopper cloth about 2.5 cm above the bottom. Traps (eight per transect) were positioned at 5 m intervals along two parallel east–west transects (separated by 20 m) and secured in place with 15 cm long metal staples driven into the ground. Because of disturbance by native animals (primarily elk, *Cervus elaphus*) during the year, not all traps could be recovered. Of 16 litter traps deployed at each site, we recovered 14–16 traps in seven of the stands, seven traps in two stands, four traps in one stand, three traps in one stand, and zero traps in three stands where all traps had been overturned or moved around. Litter from each trap was separated into four categories: pine needles, woody material, graminoids, and forbs. For comparison among stands, we computed the average dry mass of litter per trap for each site and the proportions of total litter in each litter category.

Soil N transformations

Soil samples ($n = 9$ per stand) were collected to a depth of 15 cm using a polyvinyl chloride core (5 cm diameter) along the three 50 m transects used for vegetation sampling. There was minimal forest floor material in these stands, but any litter at the soil surface was removed from the core. Soil samples were placed in plastic bags and kept cool for transport to the laboratory, where soils were combined and homogenized to create one composite soil sample per stand. Composited soils were sieved (2 mm) and shipped overnight to the University of Wisconsin-Madison for analysis.

Gross rates of NH_4^+ and NO_3^- production and consumption were calculated, using ^{15}N isotope dilution (Hart et al. 1994), on a subsample of the composited soils using 24 h soil incubations. Briefly, 1 mL of either (^{15}NH$_4$)$_2$SO$_4$, ^{15}N$_2$, 98%+ or K^{15}NO$_3$,^{15}N, 98%+ at a concentration of 30 μg N·mL^{-1} was pipetted into 30 g of soil. Solution was mixed in the soil for <10 s per sample using a vortexer to distribute the label evenly. Within 15 min of injection, 15 g of the original 30 g of soil was transferred to a new container, and 75 mL of 2 mol·L^{-1} KCl was added to create the initial ($t = 0$) sample. Samples were shaken for 30 min and filtered using KCl-rinsed Whatman No. 2 filters. The remaining soil (approximately 15 g) was incubated at a constant temperature and moisture for 24 h, long enough for the N pools to dilute isotopically but short enough that remineralization was unlikely. After the incubation period, the soil was extracted and filtered as described above. Extractants were frozen (–18 °C) until further analysis. N (NH_4^+-N and NO_3^--NO_2^--N) concentrations of all samples were determined on a Lachat QuikChem 8000 autoanalyzer (Lachat Instruments, Milwaukee, Wisconsin, USA). Samples were diffused using a ^{15}N diffusion procedure with MgO + Devarda's alloy. Samples were analyzed for isotopic enrichment at the University of California-Davis Stable Isotope Facility (Davis, California) with a Europa Scientific continuous flow mass spectrometer (PDZ Europa, Inc.).

Isotopic pool dilution allows gross production and consumption of ammonium and nitrate to be estimated separately, but it is a short-term assay. Therefore, we also include here for comparison estimates of inorganic N availability from free ion-exchange resin bags deployed in 12 of the 14 stands during 2005 as part of another study (Levitt 2006). Resin bags were made of nylon stocking material and contained 20 g of cation–anion exchange resin beads (J.T. Baker). Thirty-six free resin bags were deployed in each stand in June 2005, placed under the litter (if any was present) and slightly underneath the mineral soil, enough to prevent exposure to sunlight. Resin bags were retrieved in September 2005, refrigerated, air-dried, and extracted in 75 mL of 2 mol·L^{-1} KCl. Extracts were filtered with 0.7 μm filter paper and analyzed colorimetrically for NH_4^+-N and NO_3^--N using a flow-injected autoanalyzer (Lachat Instruments, Milwaukee, Wisconsin). Because of the difference in sampling years, we only use the resin N data to determine whether there was a significant relationship between N availability and tree density or ANPP, which were both remeasured in 2005 following the same procedures described above (Levitt 2006).

General soil characteristics

The stands were revisited during the summer of 2005 to obtain soil samples for general analysis (pH, soil organic matter, and total N) (Levitt 2006). Twenty samples of the upper 15 cm of mineral soil were collected at random locations in 12 stands; two were not accessible because of bear activity in the area. Although these samples were obtained in a different year, the general soil properties should remain relatively consistent. Soils were kept cool until transported to the field laboratory, where they were composited, homogenized, and sieved (2 mm). A 50 g subsample was air-dried and sent to the Soils and Plant Analysis Lab at the University of Wisconsin-Madison (for methods, see http://uwlab.soils.wisc.edu/).

Statistical analyses

All statistical analyses were performed using stands ($n = 14$) as the sample unit. We used paired t tests to determine whether tree density and measurements of biomass, LAI, and ANPP differed between 1999 and 2003. Pearson's correlation coefficients were computed to determine how tree size (height, basal diameter, and 2002 height increment), foliage biomass, LAI, and ANPP varied with tree density in 2003. Data were tested for normality, and tree density was log transformed, lodgepole pine ANPP was square-root transformed, and resin bag N was $\log(x + 1)$ transformed to normalize their distributions. To evaluate whether foliar N concentrations; total foliar N; and the gross production, consumption, and net production of both NH_4^+ and NO_3^- were related to tree density and ANPP, we first examined Pearson's correlation coefficients for all pairwise comparisons of variables. For the 2005 data, we examined only the relationship between N availability and 2005 tree density and ANPP (i.e., no foliar N variables) because of the difference in sampling years. Because litter inputs may have a direct effect on soil processes, we also determined whether litter quantity was correlated with ANPP or tree density and, in turn, whether the litter mass explained any of the variation in laboratory assays of soil N transformations. Because of the disturbance of the litter traps described above, these analyses were conducted using 11 of the 14 stands for which we had litter data. Finally, we used multiple regression to predict foliar N concentrations and total foliar N based on

stand characteristics (tree density and ANPP), litter variables, N transformations, and general soil characteristics ($n = 10$ stands with data on all independent variables). We used a best model selection using a maximum of three predictor variables in each model and evaluated model performance using Akaike's Information Criterion and adjusted r^2. All analyses were performed in SAS (SAS Institute Inc. 2003).

Results

Variation in tree density, ANPP, LAI, and foliage biomass

Among the 14 postfire stands, lodgepole pine density in 2003 averaged 84 333 trees·ha^{-1} (median = 11 000) and ranged from 467 to 535 000 trees·ha^{-1} (Table 1). Stand-density measurements from 1999 and 2003 were highly correlated ($r = 0.99$, $P < 0.0001$), and a paired t test revealed no significant difference in tree density between the two sampling years ($t_{13} = 0.01$, $P = 0.9927$). However, there was considerable variability in tree size and tree growth rates among stands of different density. The average 2003 tree height in the 14 stands was 136 ± 21 cm (range from 63 to 189 cm), average basal diameter was 3.2 ± 0.70 cm (range from 0.9 to 5.4 cm), and the average 2002 height increment was 16.7 cm ± 3.42 cm (range from 3 to 27 cm). Stands of greater density had trees of shorter height ($r = -0.56$, $P = 0.0373$), smaller basal diameter ($r = -0.77$, $P = 0.0012$), and smaller annual height increments ($r = -0.74$, $P = 0.0034$). The mean 2003 tree ANPP rate averaged 424 ± 224 g·tree^{-1}·year^{-1} but varied 100-fold among stands, ranging from 14.1 to 1424.0 g·tree^{-1}·year^{-1}. The per-tree ANPP rates were negatively correlated with tree density ($r = -0.61$, $P = 0.0194$). There was no relationship between tree density and total soil N or soil C/N ratio.

Total ANPP (trees + herbaceous) at the stand level averaged 6.2 ± 3.0 Mg·ha^{-1}·year^{-1} in 2003, which was a 72% increase since 1999 (3.6 ± 1.4 Mg·ha^{-1}·year^{-1}); paired t tests indicated that this increase in ANPP was significant ($t_{12} = 3.02$, $P = 0.0107$). Most (79%) of the total ANPP was contributed by *P. contorta* (4.9 ± 3.1 Mg·ha^{-1}·year^{-1}) with the remaining 21% derived from the herbaceous vegetation (1.3 ± 0.42 Mg·ha^{-1}·year^{-1}). (Postfire regrowth has been slow for the dominant shrub, *Vaccinium scoparium*, and shrub ANPP was negligible.) Total LAI averaged 2.3 ± 1.4 m^2·m^{-2} in 2003, with 99% of the leaf area attributable to *P. contorta*, which is an increase of 92% since 1999. As observed previously (Turner et al. 2004), there were positive correlations in 2003 between tree density and stand ANPP ($r = 0.58$, $P = 0.0296$) and between stand ANPP and LAI ($r = 0.94$, $P < 0.0001$). However, LAI was not correlated with tree density in 2003 ($P > 0.05$). Lodgepole pine ANPP and LAI were both negatively correlated with percent soil organic matter ($r = -0.63$, $P = 0.0267$; $r = -0.61$, $P = 0.0360$, respectively) but were not related to total soil N or soil C/N ratio.

Foliage biomass per tree in 2003 averaged 449 ± 236 g·tree^{-1} but ranged from 4.8 to 1517 g·tree^{-1} among the 14 stands. This reflected an increase of 195% since 1999, when foliage biomass averaged 152 g·tree^{-1} and ranged from 9.5 to 482 g·tree^{-1}. Foliage biomass per tree in 2003

Fig. 1. Mean foliar N concentration in new lodgepole pine needles vs. tree density for 15-year-old stands of postfire lodgepole pine. ($n = 12$ rather than 14 because current-year needle samples from two stands were inadvertently lost before processing.) The critical value of 1.2% (Moore et al. 2004) is indicated by the horizontal line.
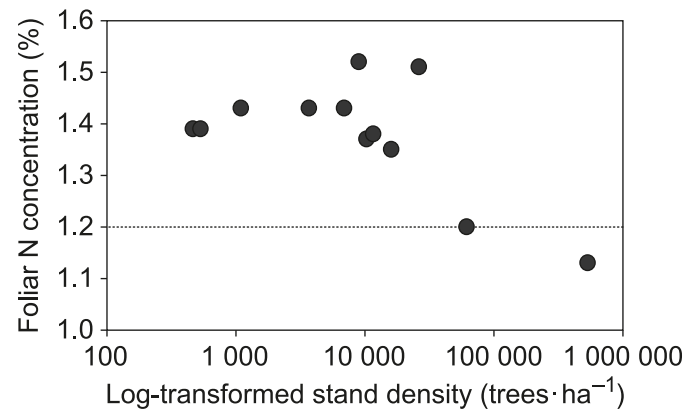
declined significantly with tree density ($r = -0.61$, $P = 0.0202$). At the stand level, lodgepole pine foliage biomass in 2003 averaged 4832 ± 314 kg·ha^{-1} and ranged from 261 to 23 085 kg·ha^{-1}, thus spanning three orders of magnitude. This foliage biomass also represented a substantial increase since 1999, when foliage biomass averaged 2527 kg·ha^{-1} and ranged from 26 to 7840 kg·ha^{-1}. Total foliage biomass per stand was not correlated with tree density ($P = 0.22$) but was positively correlated with lodgepole pine ANPP ($r = 0.93$, $P < 0.0001$). Total foliage biomass was also negatively correlated with percent soil organic matter ($r = -0.58$, $P = 0.0478$) but not with total soil N or C/N ratio.

In sum, at the stand level, ANPP increased from 1999 to 2003, but tree density did not change (i.e., no detectable self-thinning). Lodgepole pine ANPP and total foliar biomass were positively correlated, and stand-level ANPP increased with tree density. However, ANPP and foliar biomass of individual trees declined with tree density.

### Foliar N concentration and total foliar N

Foliar N in new needles

The mean foliar N concentration of new lodgepole pine needles was 1.38% ± 0.06%, which exceeds the level (1.2%) considered to indicate N limitation in lodgepole pine (Brockley 2001). In fact, foliar N of current-year needles was well above the 1.2% threshold in all but two stands, both of which had very high tree density (>80 000 trees·ha^{-1}, Fig. 1). The mean C/N ratio in the new lodgepole pine foliage was 35.6 ± 1.68 (range of 32.3 to 42.8). Foliar N concentration in new needles was negatively correlated with tree density ($r = -0.60$, $P = 0.0406$; Fig. 1), and foliar C/N ratio was positively correlated with tree density ($r = 0.65$, $P = 0.0231$). Foliar N concentration in new needles was not related to total soil N, soil organic matter, or soil C/N ratios (all $P > 0.05$).

Foliar N in composite needles

Foliar N concentration in composite (all-age) needles

Fig. 2. Mean foliar N concentration in composite (all age) lodge-pole pine foliage measured in 2003 in 14 stands that established following the 1988 Yellowstone fires versus (a) tree density and (b) stand-level lodgepole pine aboveground net primary production (ANPP).
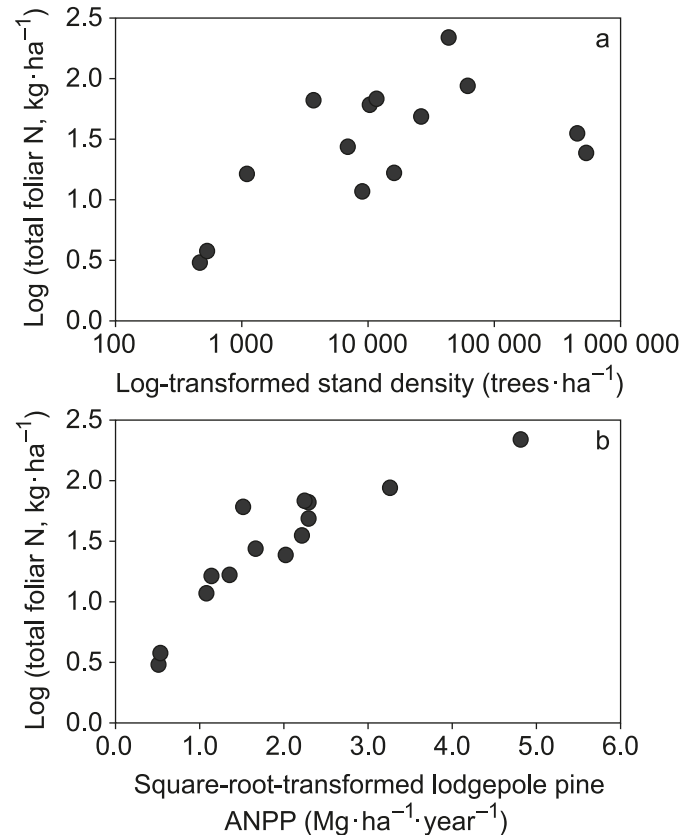

Fig. 3. Total foliar N pools estimated in 2003 in 14 lodgepole pine stands that established following the 1988 Yellowstone fires versus (*a*) tree density and (b) stand-level lodgepole pine aboveground net primary production (ANPP).
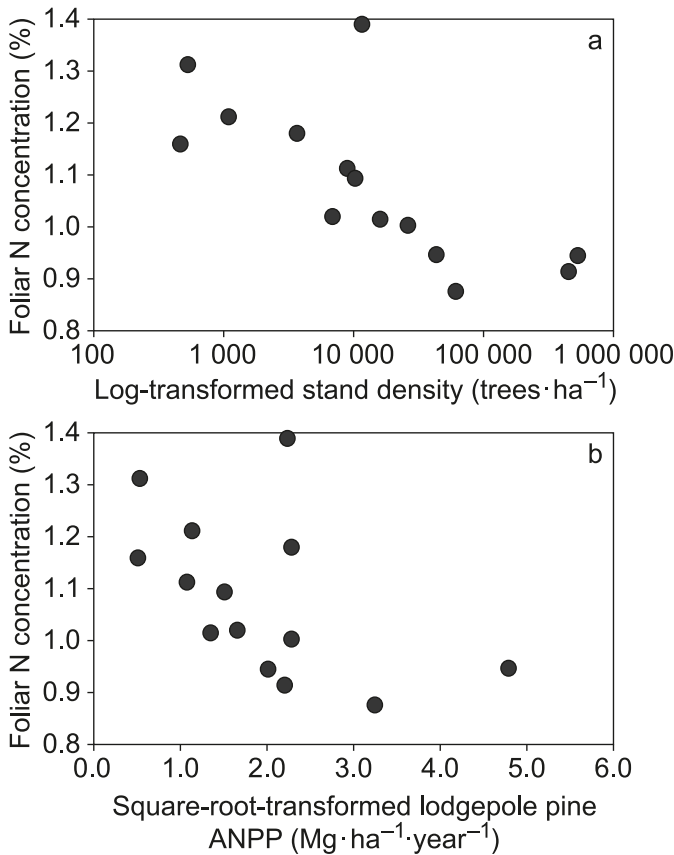
averaged 1.08% ± 0.08% and varied substantially among stands (range of 0.87% to 1.39%). The C/N ratio of composite lodgepole pine foliage averaged 48.8 ± 3.6 and also varied among stands (range of 36.5 to 59.2), largely in response to the foliar N variation; average foliar C concentration in composite samples from lodgepole pine was 50.5% ± 0.34%, thus varying minimally among stands. Composite lodgepole pine foliar N concentration was negatively correlated with both tree density ($r = -0.90$, $P < 0.0001$) and stand ANPP ($r = -0.68$, $P = 0.0068$) (Fig. 2). Neither foliar N concentration nor C/N ratio was correlated with LAI or with total soil N, soil organic matter, or soil C/N ratios (all $P > 0.05$).

Total foliar N

The lodgepole pine foliar N pool averaged 48.3 ± 29.4 kg N·ha^{-1} among stands (range from 3.6 to 218.4 kg N·ha^{-1}). Total foliar N correlated most strongly with tree ANPP ($r = 0.90$, $P < 0.0001$; Fig. 3) and also correlated positively with tree LAI ($r = 0.76$, $P = 0.0015$) and tree density ($r = 0.57$, $P = 0.0336$; Fig. 3). Thus, foliar N concentration (at the individual tree level) was most strongly related to tree density, whereas the total foliar N pool (at the stand level) was most strongly related to ANPP. Although trees in high-density stands had lower foliar N concentrations and less foliage bi-

omass per tree, they accounted collectively for substantial uptake and storage of foliar N.

Litter production, soil N transformations, and relationships with foliar N

Litter production

For the 11 stands from which litter traps were retrieved successfully, the average dry litter mass was 35.4 ± 21.7 g·m^{-2} (range 5.8 to 135.8 g·m^{-2}). About 35% of the litter was pine needles, on average, although this varied considerably among sites; one stand contained 96% pine needles. About 65% of the litter was woody material, e.g., twigs and small branches; graminoid and forb litter were both negligible. When considering only the mass of pine needle litter, the mean was 12.5 g·m^{-2}, but values ranged from 0 to 27.5 g·m^{-2}. The mass of pine needle litter was positively correlated with lodgepole pine ANPP ($r = 0.73$, $P = 0.0101$, $n = 11$) and with total lodgepole pine foliage biomass ($r = 0.61$, $P = 0.0471$, $n = 11$).
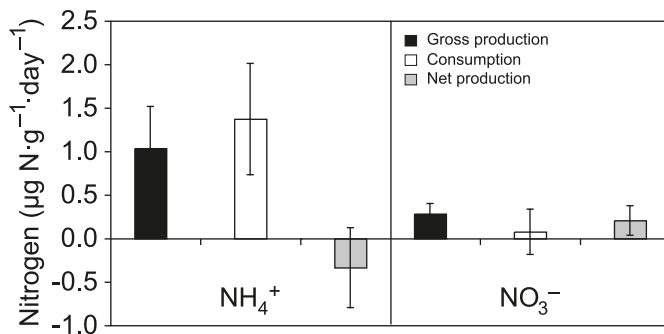
Gross production and consumption of NH_4^+

The results of the ^{15}N pool dilution showed that average consumption of NH_4^+ equaled or exceeded gross NH_4^+ production, resulting in net NH_4^+ depletion (Fig. 4). Net NH_4^+ production averaged -0.34 ± 0.46 µg NH_4^+·g^{-1}·day^{-1}, indi-

Table 2. Pearson's correlation coefficients (and P values) for gross production, consumption, and net production of NH_4^+ and NO_3^-, as measured by isotopic pool dilution; $n = 14$ stands.

	NH_4^+			NO_3^-		
	Gross production	Consumption	Net production	Gross production	Consumption	Net production
NH_4^+						
Gross production	1.0	**0.69** (0.0061)	ns	ns	0.52 (0.0522)	**–0.53** (0.0492)
Consumption		1.0	**–0.66** (0.0095)	**0.57** (0.0352)	**0.55** (0.0416)	ns
Net production			1.0	ns	ns	ns
NO_3^-						
Gross production				1.0	**0.85** (0.0001)	**–0.58** (0.0303)
Consumption					1.0	**–0.92** (<0.0001)
Net production						1.0

Note: ns, not significant. Values in bold indicate $P < 0.05$.

Fig. 4. Gross production, gross consumption, and net production of NH_4^+ and NO_3^- estimated by using ^{15}N pool dilution methods in 15-year-old stands ($n = 14$) of lodgepole pine that established after the 1988 Yellowstone fire. Error bars indicate ±2 SE.

cating substantial variability among the 14 stands, with net NH_4^+ values ranging from –1.27 to 2.24 µg $NH_4^+ \cdot g^{-1} \cdot day^{-1}$. Gross production and consumption of NH_4^+ were positively correlated with each other (Table 2). Correlation analyses identified no significant relationships for gross production, consumption, or net production of NH_4^+ with tree density, ANPP, or LAI.

Pairwise correlations indicated that gross production of NH_4^+ increased with composite foliar C/N ratio ($r = 0.63$, $P = 0.0156$) and with the mass of pine litter produced ($r = 0.61$, $P = 0.0443$) and declined with increasing total soil N ($r = –0.57$, $P = 0.0338$). In a multiple regression, however, only the composite foliar C/N ratio was retained, explaining 40% of the variation in gross NH_4^+ production. Gross consumption of NH_4^+ was also positively related to pine litter production ($r = 0.73$, $P = 0.0105$). Net production of NH_4^+ was not correlated with variables measured in this study. Thus, the results indicate that stands with a lower foliar N concentration (or higher foliar C/N ratio) and greater pine needle litter inputs were associated with greater rates of gross NH_4^+ production, and NH_4^+ consumption was greater in soils from stands having more pine litter inputs.

Gross production and consumption of NO_3^-

Results of the ^{15}N pool dilution for nitrification indicated lower rates of gross production of NO_3^- compared with NH_4^+, and very low consumption of NO_3^- (Fig. 4). Average net NO_3^- production among the 14 stands was 0.21 ± 0.18 µg $NO_3^- \cdot g^{-1} \cdot day^{-1}$, but it ranged from –1.3 to 0.88. As with ammonification, there was a positive correlation between gross production and consumption of NO_3^- (Table 2). There were no significant relationships between nitrification rates and ANPP or tree density. Gross NO_3^- production was positively correlated with NH_4^+ consumption, which is consistent with NH_4^+ providing the substrate for nitrification, whereas, NO_3^- consumption was positively correlated with both gross production and consumption of NH_4^+ (Table 2). Variables related to soil and stand characteristics, including lodgepole pine foliar N, were not significant in models for NO_3^-.

Resin bag N from 2005

Among the 12 stands for which data were available (Levitt 2006), resin bag N from the 2005 growing season averaged 3.59 ± 0.81 µg $N \cdot bag^{-1} \cdot day^{-1}$ and ranged from 0.87 to 9.29 µg $N \cdot bag^{-1} \cdot day^{-1}$. Ammonium averaged 2.57 ± 0.57 µg $N \cdot bag^{-1} \cdot day^{-1}$ (71% of the total) and ranged from 0.62 to 6.76 µg $N \cdot bag^{-1} \cdot day^{-1}$. Nitrate averaged 1.0 ± 0.26 µg $N \cdot bag^{-1} \cdot day^{-1}$ (29% of total) and ranged from 0.16 to 2.74 µg $N \cdot bag^{-1} \cdot day^{-1}$. Resin bag ammonium and total N were negatively correlated with tree density ($r = –0.58$, $P = 0.0463$; $r = –0.59$, $P = 0.0414$, respectively) but were not related to ANPP ($P > 0.05$). Resin bag nitrate was not related to tree density or ANPP.

Predicting foliar N

In stepwise multiple regression models in which predictor variables included stand structure, ANPP, litter production, soil N transformations, and general soil characteristics ($n = 10$ stands for which all predictors were available), foliar N concentration of composite foliage was predicted only by a negative relationship with (log-transformed) tree density ($r^2 = 0.93$, $F = 109.79$, $P < 0.0001$; see also Fig. 2a, which shows all 14 stands), and total foliar N pool was predicted only by a positive relationship with (square-root transformed) ANPP ($r^2 = 0.81$, $F = 33.28$, $P = 0.0004$; see also Fig. 3b).

Discussion

The results of this study indicate that the initial landscape patterns of postfire tree density, which established soon after

the 1988 fires owing to spatial variation in prefire serotiny and the severity and pattern of the fire (Turner et al. 1997), are closely associated with patterns of foliar N in the postfire landscape. Fifteen years after the fires, the densities of postfire lodgepole pine still varied dramatically across the landscape. These variable densities, in turn, are associated with large differences in ANPP, foliar N concentrations, and N retention among the postfire stands. In the context of the expectations we presented regarding N limitation, our results also suggest that N is not yet limiting in these developing stands (Table 3).

Consistent with expectations for lodgepole pine productivity to peak $\sim$40–50 years after stand establishment (Pearson et al. 1987; Olsson et al. 1998), ANPP was still increasing in these 15-year-old stands. However, the among-stand variation in productivity remained very high, and the most productive stands were stocked at relatively high density. Studies related to forest management have also found a positive relationship between stand productivity and tree density (e.g., Lindgren et al. 2007), albeit within a much more narrow range of densities (250 to >3000 trees·ha^{-1}) than those considered here. We did not measure belowground production, but ANPP is a very good indicator of NPP in these young stands because C allocation in lodgepole pine does not vary with tree age and density (Litton et al. 2004). Also, self-thinning was not yet apparent in these developing stands, including stands of highest tree density, suggesting that intraspecific competition was not yet causing mortality.

Foliar N concentrations >1.2% in the new needles suggest that most of the developing stands of lodgepole pine have not yet encountered N limitation (Table 3). Only the high-density stands (>80 000 trees·ha^{-1}), at 1.13% N, were below the critical level of 1.2% suggested by Moore et al. (2004) or at the threshold of 1.00%–1.15% indicating moderate to severe N limitation, as suggested by Brockley (2001). All other stand means were >1.3%, indicating an adequate N supply. The average foliar N concentrations we observed in these young postfire stands also exceed the values reported for unfertilized 14-year-old lodgepole pine in British Columbia (1%–1.15%, Brockley 1995) and for lodgepole pine stands in southwestern Alberta (0.93%; Prescott et al. 1989). The mean (1.38%) is in the 95th percentile for foliar N concentrations in mature lodgepole pine in the interior northwestern US (Moore et al. 2004).

Foliar N concentrations in composite (all-age) needles declined with tree density, as expected from a dilution effect (Binkley 1986; Table 3). The composite foliar N values were comparable to those reported by Litton et al. (2004) for 13-year-old postfire lodgepole pine in Yellowstone, who also observed decreasing foliar N concentration with increasing stand density. Our values are lower than concentrations reported for 3- to 5-year-old lodgepole pine seedlings (1.87%) that established after fires during the summer of 2000 in our study region (Romme et al. 2009).

Although foliar N concentrations at the individual tree level declined sharply with increasing tree density, total foliar N pools at the stand level showed a strong positive correlation with ANPP and tree density. Individual trees were smaller in size and had less foliage per tree and smaller growth rates in higher density stands, but the dense stands were very productive and appear to be a significant sink for

N. Indeed, lodgepole pine foliage contained as much as 218 kg N·ha^{-1} by 2003. This positive association suggests that N is not limiting (Table 3), suggesting luxury consumption of N in these young stands.

Neither ANPP nor foliar N was strongly related to N mineralization rates in the soil, as measured in laboratory assays (Table 3). Furthermore, inorganic N availability, as measured by in situ resin bags deployed for a full growing season, also was not related to ANPP (Table 3). Among the N mineralization variables measured by pool dilution, only gross production of NH_4^+ showed any significant correlation with foliar chemistry, with greater gross production in stands with a higher foliar C/N ratio. These laboratory N mineralization rates also were not related to the total foliar N pool. Gross production and consumption of ammonium both increased with lodgepole pine litter mass, consistent with expectations for immobilization to be associated with decomposition of low-quality litter (e.g., Binkley 1986). Because soil C pools are similar among 13-year-old postfire lodgepole pine stands of differing density (Litton et al. 2004), perhaps the availability of labile C sources (i.e., new litter) could be limiting N transformations. Other studies have also shown a lack of correlation between soil nutrient supply and plant foliar chemistry. For three conifer species (balsam fir, hemlock, red spruce) in the White Mountains, there was no relationship between foliar N (%) and annual N mineralization (Ollinger et al. 2002). In an alpine community, foliar N and P concentrations in three herbaceous plants were not correlated with the rates of soil N and P supply as measured by ion exchange resin bags (Bowman et al. 2003). Belowground nutrient storage and use of organic N by plants were suggested as possible explanations for this lack of relationship (Bowman et al. 2003).

The absence of any relationship between the soil N transformations we measured and lodgepole pine ANPP and the total foliar N pool suggests that the lodgepole pine trees may be accessing another source of N. Ectomycorrhizal fungi play a role in nutrient acquisition in lodgepole pine (Douglas et al. 2005), and organic nutrients may be important for plant nutrition (Neff et al. 2003). Thus, organic sources of N could be more important for lodgepole pine than previously recognized; in Scots pine (*Pinus sylvestris*), uptake of organic N sources was equal to or greater than uptake of NH_4^+ (Persson et al. 2006). An intriguing recent study has also suggested that associative N fixation might occur within tuberculate (nodule-like) structures on some ectomycorrhizae associated with lodgepole pine (Paul et al. 2007). This study suggests a previously unrecognized potential source of N that should be investigated.

It is notable that our data indicate net positive nitrification in these 15-year-old stands; in the laboratory assays, gross production of nitrate exceeded consumption, and in the free resin bags, nitrate was approximately 28% of the total inorganic N. Resin bags deployed for a year in a chronosequence of lodgepole pine stands in Yellowstone indicated an annual average of 0.97 + 0.09 µg N·bag^{-1}·day^{-1}, of which nitrate accounted for 65% of total resin-sorbed N (Smithwick et al. 2009). Furthermore, total resin-sorbed N (NH_4^+ + NO_3^-) and resin-sorbed NO_3^- increased with stand age and decreased with tree density (Smithwick et al. 2009). Recent studies indicate that nitrification may be enhanced

Table 3. Synthesis of results in terms of expectations (see Methods), the observed results, and the interpretation with respect to a suggestion of whether inorganic nitrogen (N) may or may not be limiting lodgepole pine growth in 14 stands.

Response	Expectations	Result	Interpretation
Foliar N concentration (%N)			
New needles	If N was limiting, stands would be below the critical value (1.2%), and %N would decline with increasing density; if N was not limiting, stands would be above the critical value.	Foliar N concentration in new foliage was >1.2% (above the threshold) in 10 or 12 stands; concentration declined in two stands with highest densities (>80 000 trees·ha^{-1}).	No N limitation in most stands, but those with tree densities >80 000 trees·ha^{-1} may be approaching N limitation.
Composite needles	If N was limiting, foliar N concentration would decrease with increasing tree density (dilution of limited resource); if N was not limiting, no difference (adequate supply) or decline with density (dilution effect).	Foliar N concentration decreased with increasing tree density.	Equivocal; could be either dilution effect or N limitation.
Total lodgepole pine foliar N (kg·ha^{-1})	If N was limiting, no relationship with tree density (finite pool available for uptake, regardless of density); if N was not limiting, total foliar N would increase with tree density (more trees acquire more N).	Total foliar N increased with tree density.	N is not limiting ANPP.
ANPP vs. net N mineralization (pool dilution)	If N was limiting, ANPP should increase with net N mineralization, especially net ammonification; if N was not limiting, no relationship (other factors would control ANPP).	No relationship between ANPP and net N production of either ammonium or nitrate.	Suggests inorganic N is not limiting ANPP, but N assay was short term.
ANPP vs. N availability (free resin bags)	If N was limiting, ANPP should increase with inorganic N availability; if N was not limiting, no relationship (other factors would control ANPP).	No relationship between ANPP and N availability; negative correlation between N availability and tree density.	Inorganic N is not limiting ANPP.
Total foliar N vs. net N mineralization (pool dilution)	If N was limiting, foliar N should increase with net N mineralization; if N was not limiting, no relationship.	No relationship between total foliar N and N mineralization rates.	Suggests inorganic N availability is not limiting total foliar N pool, but N assay was short term.

by fire because of charcoal deposition (e.g., DeLuca et al. 2006), and DeLuca and Aplet (2008) estimated that the 1988 Yellowstone fires yielded approximately 3.25 Mg C·ha^{-1} as charcoal. Given the longevity of charcoal in forest soils, it is possible that persistent black C acts to keep nitrification rates elevated during secondary succession following stand-replacing crown fires.

Recent studies have suggested an important shift from microbial to vegetation control of the N cycle during succession (Chapman et al. 2006; Hart et al. 2005). In a previous study, we found substantial immobilization of NH$_4^+$ by soil microbes immediately after stand-replacing fire (Turner et al. 2007), suggesting an important microbial control on N cycling. In the current study, we have demonstrated that the forest canopy in developing postfire lodgepole pine forests can act as a strong N sink. Thus, our results support the importance of vegetation as an N sink in rapidly growing forests (Hart et al. 2005). However, our results also indicate that the strength of the N sink varies substantially across the postfire landscape as a function of tree density. In a study of 17-year-old stands of postfire lodgepole pine (in which 13 of our study stands were included), Levitt (2006) found that inorganic N availability, as measured using ion exchange resin bags, declined sharply with increasing ANPP (and tree density). Given the amount of N now sequestered in lodgepole pine foliage, as we report here, and the concomitant decline in soil N availability in stands of high density (Levitt 2006), the data suggest that the rapidly growing trees are very effectively acquiring N resources in the soil.

Understanding the spatial and temporal variability in factors limiting lodgepole pine productivity remains an important challenge. Although lodgepole pine is often considered to be N limited, experimental results have been ambiguous (see Introduction). Fertilization studies have demonstrated limitation by other nutrients, such as sulfur or boron (e.g., Brockley 2003; Blevins et al. 2005). Litton et al. (2003) also found that soil moisture declined with increasing stand density in 13-year-old postfire lodgepole pine, suggesting competition for water could be important. Thus, N may not be the only or even the key limiting nutrient for postfire lodgepole pine growth.

The initial postfire patterns of lodgepole pine density in YNP create a long-term legacy for stand structure and function for decades to centuries (Kashian et al. 2005; Smithwick et al. 2005b). The data we present here augment previous studies by demonstrating that foliar N concentrations and storage also respond strongly to the initial pattern of stand density. Foliar N concentrations were generally above critical levels, and 93% of the burned landscape has postfire lodgepole pine densities <50 000 trees·ha^{-1} (Turner et al. 2004) and thus less likely to have foliar N concentrations below the critical values. Collectively, the results suggest that N is not limiting in most of the early secondary successional stands developing after the 1988 Yellowstone fires (Table 3), although N dynamics may change through the phases of stand development. We conclude that the landscape mosaic of tree density, which was determined primarily by prefire serotiny and by the spatially variable patterns of fire severity and patch sizes and not by soil conditions (Turner et al. 1997), leaves a lasting legacy for nutrient dynamics.

Acknowledgements

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