Foliar nitrogen patterns following stand-replacing fire in lodgepole pine (*Pinus contorta* var. *latifolia*) forests of the Rocky Mountains, USA

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Abstract

Little previous work has been conducted on effects of natural, high-severity wildfires on nitrogen (N) dynamics. We measured aboveground plant biomass, foliar N, and net N mineralization 2 years after stand-replacing fires in lodgepole pine (*Pinus contorta* var. *latifolia*) forests in Grand Teton National Park, Wyoming, USA. We detected a five-fold difference in foliar N (% dry weight) among 14 species, from 0.77% in the native grass *Calamagrostis rubescens*, to 3.4% in the native N-fixer *Lupinus argenteus* and the non-native forb *Lactuca serriola*. We also observed higher foliar N in the burned stands for four of six species that occurred in both burned and unburned areas. Mean net N mineralization ranged from -23 to $+27$ mg-N kg soil^{-1} year^{-1}, and was predominantly NO_3^-. However, total biomass and foliar N, for all species combined, showed no relationships with site, fire severity, or net N mineralization—possibly because of (i) lack of inorganic N limitation, (ii) methodological shortcomings, (iii) spatial structure existing at different scales than we measured, or (iv) insufficient plant biomass at this early stage of post-fire development to respond to local variation in N availability.

1. Introduction

Foliar nitrogen (N) concentration is a useful general indicator of plant nitrogen status because it tends to be positively correlated with various measures of photosynthetic capacity, respiration, and overall physiological activity (e.g., Field and Mooney, 1986; Ryan, 1991, 1995; Reich et al., 1997; Chapin et al., 2002; Vose and Ryan, 2002). Foliar N concentrations vary substantially at multiple levels, from biomes (McGroddy et al., 2004) to species to individual plants, in response to such factors as variation in morphology, tissue age, and local N availability. Local N availability is influenced by many factors, including soil characteristics, litter chemistry, temperature and moisture conditions, and composition of the microbial community. Disturbance, e.g., by fire, also has important but complex and variable effects on N availability and plant responses. Total ecosystem N may be reduced during fire as organic N is converted to gaseous forms, but fire-induced changes in organic matter pools, soil temperature and moisture, plant uptake, and microbial activity, as well as direct production of NH_4^+ through pyrolysis, may result in a transient post-fire increase in N availability to plants (e.g., Ahlgren and Ahlgren, 1960; Wan et al., 2001; Smithwick et al., 2005).

Although N dynamics following low-severity fire have been well studied in many ecosystems (e.g., Wan et al., 2001; Hart et al., 2005), surprisingly little is known about the effects of high-severity, stand-replacing fires—which dominate the fire regimes of many extensive coniferous forest types, including boreal and subalpine forests (Smithwick et al., 2005). Yet, understanding the consequences of wildfire for vegetation dynamics and biogeochemical cycling in coniferous forest ecosystems is increasingly important, given that these systems are thought to be N-limited, and that fire frequency and severity are likely to increase with projected climate change (Dale et al., 2000; Flannigan and Wotton, 2001).

In this paper we report on foliar N content of early seral plant communities, 2 years after natural stand-replacing fires in

lodgepole pine (*Pinus contorta* var. *latifolia*) forests in the Rocky Mountains, USA. The fires were ignited by lightning, and burned during dry conditions in late summer of 2000. Although the fires killed all aboveground biomass in the areas where we worked, there was important spatial variability in fire severity, similar to what was observed in the extensive 1988 Yellowstone fires (Turner et al., 1994, 1997, 1999): in some places the fire burned in the canopy and consumed all leaves and small twigs (crown fire), but in other places an intense surface fire scorched and killed, but did not consume, the canopy (severe surface fire). We measured foliar N concentration and peak standing crop biomass in all of the dominant post-fire species, as well as an index of soil inorganic N availability (net N mineralization rate) in two study sites. Both sites were similar in terms of elevation (ca. 2150 m), topography (gently rolling), soils (poorly developed Inceptisols), pre-fire vegetation (montane and subalpine conifers), and synoptic climate (cool temperate), but exhibited subtle differences as well: one site supported 120–150-year old forests on an infertile substrate, while the other was covered by forests >200-year old on a somewhat more fertile substrate. We evaluated patterns in foliar N both at the species level (comparing individual species) and at the stand level (summing biomass and N content of all species and expressing on a per hectare basis), and we compared these patterns with variation in stand-level soil inorganic N availability. For those species that were dominant in burned areas and also occurred in unburned forests, we compared foliar N concentrations in burned and nearby unburned stands. Three specific questions were addressed:

(1) *Do foliar N concentrations differ among dominant species after fire?* We predicted that foliar N would be highest in symbiotic N-fixers, because they potentially have an abundant N supply, recognizing that there are significant energetic constraints in utilizing this N source (Chapin et al., 2002). We further predicted that foliar N would be intermediate in non-fixing species that are most abundant in recently disturbed habitats (early seral species), because these species are thought to have relatively rapid growth rates and high N requirements that are met by the presumably high availability of inorganic nitrogen soon after a fire. Finally, we predicted the lowest foliar N concentrations in species that are more common in old forests (late seral species). These stress-tolerant species are thought to grow relatively slowly, with lower N requirements, even when they occur at low abundance in recently burned areas.

(2) *Do foliar N concentrations in dominant post-fire species differ between burned and unburned forests at the same site?* We predicted that, for a given species, foliar N concentration would be higher in the burned areas than in adjacent unburned areas, because of a presumably greater availability of inorganic N in the burned areas.

(3) *Do total aboveground biomass, foliar N, and foliar N content by species differ by site, soil nitrogen availability, or fire severity?* We predicted that stand-level total biomass and total foliar N content would be highest in the more fertile study site, in stands having greater net N mineralization,

and in stands burned by surface fire rather than crown fire. We further predicted that, for a given species, foliar N concentration would be higher in the more fertile study site, in stands having greater net N mineralization, and in stands burned by surface fire. The presumed mechanism underlying these predictions is that all of these situations would be associated with greater inorganic N availability.

1.1. Study area

The study took place in Grand Teton National Park (GTNP) and the adjacent Rockefeller Parkway (administered by GTNP) in northwestern Wyoming, USA. Our first study site was the 1280 ha Glade Burn in the Rockefeller Parkway, which affected primarily mature forests on infertile substrates. This site was dominated by a mosaic of 120- and 150-year old lodgepole pine forests that had developed following previous stand-replacing fires in 1879 and 1856. The substrate consisted of quaternary rhyolite bedrock and rhyolite-dominated glacial deposits, and soils were mostly Typic Cryumbrepts and Dystric Chryocrepts. The second study site was the 840 ha Moran fire on the western shore of Jackson Lake, which burned older forests on somewhat more fertile substrates. This site was dominated by a mix of lodgepole pine, Engelmann spruce (*Picea engelmannii*), and subalpine fir (*Abies lasiocarpa*), and had not burned for at least 200 years (possibly much longer). The substrate consisted of glacial moraine deposits, containing material from Precambrian crystalline rocks as well as Paleozoic sedimentary rocks, and soils were mostly Typic Chryocrepts. Both sites were at ca. 2150 m elevation on gently rolling topography. The nearest weather station is at Moran, WY, ca. 25 km away in the same mountain valley as the two study sites. This station has recorded average air temperatures of $-9.6\,^{\circ}$C in December and 16 $^{\circ}$C in July, and average annual precipitation of 575 mm. Although one flank of the Glade fire was actively suppressed to protect park developments, most of the area (including our study site) burned without interference. Because fire retardant typically contains inorganic N, we were careful to select a study area where no fire retardant was applied. The Moran fire burned entirely without interference and with no retardant application.

At each site, we established five permanently marked 0.25 ha stands in 2001, 1 year after the fires. Two stands at each site were placed in areas of crown fire, and three were in areas of severe surface fire. Nevertheless, all 10 stands were located within stand-replacing burns in which all of the trees were killed and most of the litter layer was consumed. Soils in all stands had essentially no O horizon, other than a shallow sprinkling of fallen scorched needles in the surface-fire stands. Except for these differences in fire severity, all five stands at a site were similar with respect to topography and pre-fire vegetation structure, and represented typical conditions for the burned site as a whole. In each stand, a 50 m transect was extended north through a relatively homogeneous-appearing area. A parallel 50 m transect also was established at a distance of 25 m on either side of the central transect, thus demarcating a 50 m × 50 m stand.

2. Methods

2.1. Soils analysis

To characterize and compare soil chemistry and general nutrient content of the two study sites, 20 samples of the upper 15 cm of mineral soil were collected in a random fashion from each of the five burned stands at each site, homogenized and composited into one sample per site, then air dried and sent to the Soils and Plant Analysis Lab at the University of Wisconsin, Madison for determination of general soils characteristics. Total C was determined by dry combustion using the Tekmar-Dohrman 183 TOC Boat Sampler DC-190 (Tekmar-Dohrman, Mason OH). A micro-Kjeldahl procedure was used for total N determination (Jackson, 1958). Acid extractable P was analyzed colorimetrically using the Truog method, and potassium (K), calcium (Ca), and magnesium (Mg) were measured by atomic absorption after extraction with H_2SO_4. Soil pH was measured in water with a 1:1 mass:volume ratio (Schulte et al., 1987).

2.2. Foliar N concentrations

All vegetation sampling was conducted in early August, 2002, when herbaceous cover was at or near its maximum for the year, but the plants had not yet begun to show signs of senescence. The dominant species at each site were identified on the basis of an initial visual estimate of percent cover of all species present. Ten samples of each dominant species were randomly collected from the burned areas, adjacent to but not within the 0.25 ha stands. Sampled individuals of each species were separated by at least 5 m, and only plants with fully expanded green leaves were collected. One such set of 10 samples per species was collected from the general burned area to characterize foliar N at each site (Glade and Moran), but individual stands within each site were not sampled separately. Adjacent unburned forest was searched for the species collected in the burned area, and these species were also sampled in the unburned forest if available, in locations at least 50 m from the burned edge. Plant samples were placed in a cooler with ice and returned to the lab where the fully expanded leaves from individuals were separated from dead tissue. Only current year's green leaves were saved. Foliar tissue samples were oven-dried for 24 h at 70 °C to constant mass, kept dry, ground and analyzed for N concentration on a LECO CHN dry-combustion analyzer (LECO, St. Joseph, MI).

2.3. Total biomass and foliar N at species and stand levels

Percent cover of each species (to the nearest 10% if >10%, or to the nearest 1% if <10%) was estimated visually by a single observer within eight 0.25 m^2 quadrats positioned at 5 m intervals along the stand's two outer transects, and nine quadrats positioned similarly along the center transect ($n = 25$ quadrats per stand), and mean % cover was computed for each species. We then used species-specific allometric models, previously developed by harvesting vegetation within similar post-fire stands in nearby Yellowstone National Park (Turner et al., 2004), to estimate aboveground biomass for each species. These allometric models predict aboveground biomass (g m^{-2}) from % cover with r^2 values of 0.84–0.99. Biomass was summed across all species to arrive at total aboveground biomass per hectare. Stand-level N content (kg-N ha^{-1}) was determined by first multiplying foliar N concentration of each species by the species' total biomass in the stand, then summing all individual species' foliar N. Our allometric equations predicted total aboveground biomass, including stems, flowers, fruits, and leaves, whereas our foliar N concentrations were derived from leaves alone. This no doubt led to some overestimation of total stand-level N (kg ha^{-1}), because leaves tend to have substantially higher foliar N concentrations than other plant tissues. However, leaves were by far the major component of aboveground biomass in all of the species that we sampled in all 10 burned stands, so the magnitude of this error probably is small. We did not estimate total aboveground biomass or stand-level foliar N in the unburned stands, but only measured N concentration of leaves for comparison with individual plants in the burned stands.

To scale up from individual species to stand-level responses, we first examined the proportion of total plant cover in each stand that was comprised of species for which we had allometric relationships between cover and biomass as well as measurements of foliar N concentration. The species for which we had this information comprised >90% of total plant cover (91.3–99.6%) in eight stands. In the other two stands, cover of species for which we had adequate measurements was <90%, i.e., >10% of total cover was of species for which we lacked allometric equations or foliar N measurements. Therefore, these latter two stands (both with surface fire at the Glade site) were deleted from the stand-level analyses. However, all 10 stands were used for analyses of individual species responses and comparisons of N mineralization rates.

2.4. In situ N mineralization

The resin core incubation method (Binkley and Hart, 1989; Binkley et al., 1992) was used to estimate rates of net N mineralization in situ in each 0.25 ha burned stand for the year preceding our foliar N sampling (i.e., from July 2001 to July 2002). Ten resin cores were placed along each of two parallel transects running east-west and located in the center of each stand, for a total of 20 cores per stand. Transects were 8 m apart, and cores were separated by 2 m along each transect. Incubations used open PVC tubes, 5 cm in diameter and 15 cm deep, buried such that the top of the tube was flush with the soil surface, with a resin bag at the bottom (Binkley et al., 1992; DiStefano and Gholz, 1986; Strader et al., 1989). The resin cores were open to water flow, thereby allowing the products of mineralization to leach from the soil column into the resin bags.

Resin bags contained 20 g dry mass of mixed bed exchange resin (J.T. Baker #4631) in commercial nylon stocking material. Initial soil samples were collected to the same depth (15 cm) adjacent to each resin core using a clean PVC tube. The

soil was homogenized, and a 20 g sub-sample was extracted in 75 ml of 2 M KCl to determine initial ammonium and nitrate levels at the onset of incubation. All samples were processed within 24 h of return to the lab, homogenized, weighed, extracted in 2 M KCl by shaking the sample for 1 h and then filtered after a brief settling time (between 1 and 3 h). Extracts were filtered with 0.7 μm sample-rinsed filter paper.

At the end of the 1-year incubation, the resin bags and the soil within the PCV tube above the bag were collected and returned to the lab. The soil was homogenized and weighed, then a 20 g sub-sample was extracted in 75 ml 2 M KCl. The resin bags also were extracted with 50 ml of 2 M KCl. Extracts were subsequently analyzed colorimetrically for nitrate and ammonium using a flow-injected autoanalyzer (Lachat Instruments, Milwaukee, WI). Soil moisture content was determined for the pre- and post-incubation soils by oven-drying at 105 °C for 24 h. Net N mineralization was calculated as the post-incubation quantity of NH_4^+ plus NO_3^- in the soil and resin bag combined, minus the quantity in the pre-incubation soil, expressed as mg-N per kg-soil per year.

2.5. Statistical analysis

All variables were tested for normality by constructing quantile–quantile (QQ) plots and visually estimating the fit to the QQ-line and checking residuals for normality. Log transformations were made when residuals did not exhibit a normal distribution. Analysis of variance was employed to determine if significant differences in foliar N concentrations (% dry weight) existed among species. If differences were found to be significant, Tukey's all pair-wise comparison test was used to distinguish which species were different from one another. Differences in mean concentration of foliar N of species sampled in burned and unburned sites were determined using a Welch modified two-sample *t*-test. Analysis of variance also was used to test for differences among stands in aboveground biomass and total foliar N (kg ha^{-1}) content of individual species and of all species combined. Regression analysis was used to test for relationships between net N

mineralization (independent variable) and total biomass of each species, biomass of all species combined, total foliar N of each species, and total foliar N of all species combined. All statistical analyses were carried out using PCOrd and Splus software (Insightful, Inc.) or Statistix8 (Analytical Software, Tallahassee, FL).

3. Results

Soils analyses verified our initial assumption that total nutrient concentrations were higher in the Moran site than in the Glade site, though the differences were small. The Moran site had higher soil P, Ca, and Mg, but the two sites did not differ in soil pH, % organic matter, total K, or total N (Table 1).

Fourteen species comprised most of the aboveground biomass 2 years post-fire in the two study sites. Three were graminoids (*Carex rossii*, *C. geyeri*, and *Calamagrostis rubescens*), and were common to abundant in both areas. Six were forbs, of which four were common in both areas (*Lactuca serriola*, *Lupinus argenteus*, *Epilobium angustifolium*, *Arnica cordifolia*), and two were common only in the Glade site (*Solidago multiradiata* and *Achillea millefolium*). The remaining five were low shrubs, of which one (*Spiraea betulifolia*) was common in both sites. One shrub was common only in the Glade site (*Vaccinium scoparium*), and three were found primarily at Moran (*Ceanothus velutinus*, *Lonicera utahensis*, and *Mahonia repens*). Although these shrub species can develop a moderate amount of woody tissue at maturity, at this stage they were predominantly herbaceous, i.e., composed mainly of leaves and green stems. Conifer tree seedlings were present, but very small (<5 cm tall), and constituted a negligible component of total aboveground biomass. Some dozen other herbaceous species also were present, but all in very low densities and with very little total biomass.

3.1. Question 1. Do foliar N concentrations differ among dominant species after fire?

Foliar N concentrations (% dry weight) differed significantly among the 14 species sampled (Fig. 1). Data were aggregated

Table 1

Soil chemistry and other site characteristics at the infertile Glade site in Rockefeller Parkway, and at the relatively more fertile Moran site in Grand Teton National Park, Wyoming, USA

	Glade site	Moran site	P
Elevation (m)	2135	2150	
Substrate and soils	Rhyolite bedrock and rhyolite-derived glacial deposits. Typic Cryumbrepts and Dystric Chryocrepts	Glacial deposits from crystalline and sedimentary rocks. Typic Chryocrepts	
Pre-fire vegetation	120- and 150-year old lodgepole pine forests	>200-year old forests of lodgepole pine, Engelmann spruce, and subalpine fir	
Soil pH	5.64	5.64	NS
% soil organic matter	3.64	4.40	NS
Soil K (kg ha^{-1})	473	497	NS
Total soil N (% dry weight)	0.1	0.1	NS
Soil P (kg ha^{-1})	16.2	52.9	0.003
Soil Ca (kg ha^{-1})	1251	2511	0.006
Soil Mg (kg ha^{-1})	153	247	0.0003

The column "*P*" reports alpha values for differences between the two sites using the Welch modified two-sample *t*-test. NS means non-significant (*P* > 0.05).
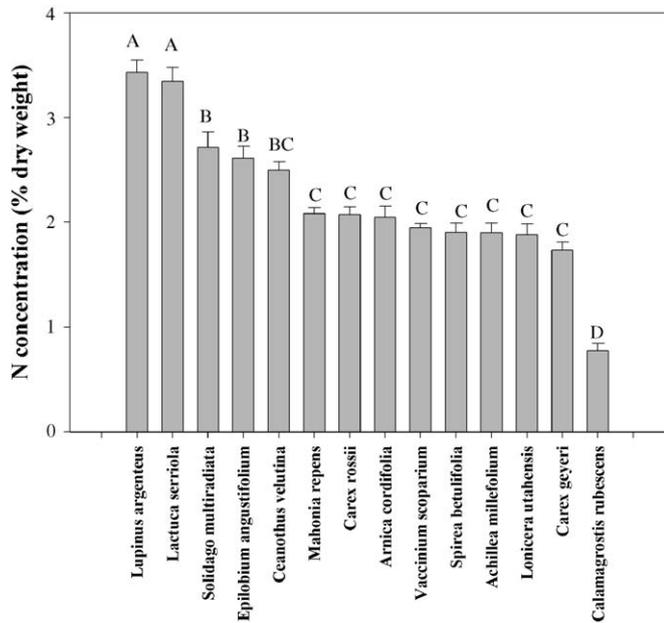
Fig. 1. Foliar N concentrations (% dry weight) in 14 species of herbs and low shrubs that comprise most of the biomass 2 years after stand-replacing fire in lodgepole pine and mixed conifer forests of Grand Teton National Park, Wyoming, USA.

(around 2% dry weight) with no significant differences among this group (Fig. 1).

3.2. Question 2. Do foliar N concentrations differ between burned and unburned forests?

Six species in the burned stands at the Glade site also occurred in nearby unburned forest. Three of these species (*Arnica cordifolia*, *Carex geyeri*, and *Vaccinium scoparium*) had higher foliar N concentrations in the burned areas than in the unburned areas (Table 2). The other three species (*Epilobium angustifolium*, *Lupinus argeneus*, and *Solidago multiradiata*) did not differ significantly between the unburned and burned forests. At the Moran site, two species in the burned stands also were present in nearby unburned stands. Of these, *Carex geyeri* had higher foliar N concentration in the burned area, whereas *Lonicera utahensis* showed no significant difference (Table 2). All three species for which foliar N concentration differed significantly between burned and unburned areas were species having relatively low foliar N, compared with the other species examined in this study (Fig. 1), and were species typically most abundant in late seral stages of forest development. Three of the four species that did not differ between burned and unburned areas were among those with the highest foliar N concentrations (Fig. 1), and are usually associated with early seral stages. The difference in foliar N concentration between burned and unburned areas was substantial for *Arnica cordifolia* and *Carex geyeri* (approximately half again as high in the burned area), but only modest for *Vaccinium scoparium* (Table 2).

3.3. Question 3. Do total aboveground biomass, foliar N, and foliar N content by species differ by site, soil nitrogen availability, or fire severity?

Total aboveground biomass (kg ha^{-1}) and total foliar N (kg N ha^{-1}) were highly correlated at the stand level, for each species individually and for all species combined. However,

across the two burned sites for those species common in both areas. The highest foliar N was found in two species—*Lupinus argenteus*, a native symbiotic N-fixing forb, and *Lactuca serriola*, a non-native non-fixing forb commonly associated with disturbed areas. Mean concentrations in these two species were ca. 3.4% dry weight. Next highest were *Solidago multiradiata* and *Epilobium angustifolium*, both native forbs associated with disturbed sites but also present at low density in old forests, with mean concentrations of 2.7–2.8% dry weight. The lowest mean N concentration (0.77% dry weight) was in a native grass, *Calamagrostis rubescens*, which grows in both disturbed and undisturbed habitats. The remaining 10 species exhibited intermediate foliar N concentrations

Table 2

Comparison of foliar N concentrations in dominant plant species of burned and adjacent unburned stands in Grand Teton National Park and Rockefeller Parkway, northwestern Wyoming, USA, 2 years post-fire

	Foliar N (% dry weight)		Foliar N group in Fig. 1	Seral stage of greatest abundance
	Burned	Unburned		
Glade site				
Arnica cordifolia[*]	2.40 (0.12)	1.50 (0.05)	C (low N)	Late
Carex geyeri[*]	1.61 (0.10)	0.96 (0.04)	C (low N)	Late
Vaccinium scoparium[*]	1.94 (0.06)	1.76 (0.04)	C (low N)	Late
Epilobium angustifolium	2.18 (0.20)	2.21 (0.11)	B (high N)	Early
Solidago multiradiata	2.71 (0.15)	2.34 (0.12)	B (high N)	Early
Lupinus argenteus	3.36 (0.16)	3.66 (0.12)	A (highest N)	Early
Moran site				
Carex geyeri[*]	1.91 (0.12)	1.22 (0.12)	C (low N)	Late
Lonicera utahensis	1.87 (0.10)	1.74 (0.06)	C (low N)	Late

Numbers in the second and third columns are means with standard errors in parentheses. Asterisk denotes significant difference in foliar N between burned and unburned stands ($P < 0.05$, Welch modified two-sample *t*-test). The fourth column refers to the four groups of species having significantly different foliar N concentrations in the burned stands (Fig. 1). The fifth column indicates whether a species is typically most abundant in early or late seral stages of conifer forests in this area (based on personal observations).

Table 3
Foliar N concentrations of 14 dominant post-fire species in burned forests of Grand Teton National Park and Rockefeller Parkway, northwestern Wyoming, USA, 2 years post-fire

	Foliar N (% dry weight)	
	Glade	Moran
Graminoids		
Calamagrostic rubescens	0.85 (0.13)	0.70 (0.05)
Carex geyeri	1.61 (0.10)	1.91 (0.12)
Carex rossii	1.96 (0.10)	2.18 (0.10)
Forbs		
Achillea millefolium	1.91 (0.10)	–
Arnica cordifolia[*]	2.40 (0.12)	1.69 (0.09)
Epilobium angustifolium[*]	2.18 (0.20)	2.83 (0.12)
Lactuca serriola	3.12 (0.20)	3.57 (0.15)
Lupinus argenteus	3.36 (0.16)	3.41 (0.15)
Solidago multiradiata	2.71 (0.15)	–
Shrubs		
Ceanothus velutinus	–	2.49 (0.08)
Lonicera utahensis	–	1.87 (0.10)
Mahonia repens	–	2.08 (0.06)
Spirea betulifolia	–	1.89 (0.10)
Vaccinium scoparium	1.94 (0.06)	–

The Glade site is infertile; the Moran site is somewhat more fertile (Table 1). Both sites experienced stand-replacing fire in 2000. Numbers are means with standard error in parentheses. Asterisk denotes the two species exhibiting a significant difference ($P < 0.05$) between sites.

neither total biomass nor total foliar N was significantly correlated with site, fire severity, or net N mineralization, either for individual species or for all species combined (data not shown). Moreover, five of the seven species common in both the Glade and Moran sites exhibited no significant differences in foliar N concentrations between the sites. However, *Arnica cordifolia* had higher foliar N concentration at the infertile Glade site, and *Epilobium angustifolium* had higher foliar N concentration at the somewhat more fertile Moran site (Table 3).

Several other interesting patterns were observed at the stand level and seemed to make ecological sense, but were non-significant ($P > 0.05$). The non-significant P values may reflect a genuine lack of difference, but could be due instead to small sample sizes and high variance (Table 4), and so are worth mentioning briefly if only to encourage further studies. Mean total biomass (kg ha^{-1}) and mean total foliar N (kg N ha^{-1}) appeared twice as high at Glade as at Moran. Mean net N mineralization (mg N kg soil^{-1} year^{-1}) appeared higher at Glade, although inorganic N at the end of the incubation was predominantly NO_3^- at both sites. We found a small net gain in soil NH_4^+ at Glade but a net loss of NH_4^+ at Moran, and NO_3^- appeared higher at Moran (Table 4). Mean total biomass and mean total foliar N appeared twice as high in the surface fire stands as in the crown fire stands, but mean net N mineralization and mean net NO_3^- appeared higher in the crown fire stands.

4. Discussion

4.1. Question 1. Do foliar N concentrations differ among dominant species after fire?

We detected a five-fold difference in foliar N concentration among the 14 common post-fire species tested, from a low of 0.77% dry weight in *Calamagrostis rubescens* to a high of 3.4% in *Lupinus argenteus* and *Lactuca serriola* (Fig. 1). Given that *Lupinus argenteus* is a symbiotic N-fixer (and we observed root nodules on excavated individuals), we partially supported our prediction that N-fixers would have the highest foliar N. However, foliar N concentration of the other potential N-fixer, *Ceanothus velutinus*, was only intermediate. This may be because the 2-year old *Ceanothus* seedlings in our study sites had not yet begun symbiotic N-fixation; in fact, isotopic ratios in the leaves (data not shown) indicated a non-atmospheric source of nitrogen.

Our second prediction – that species associated with recently disturbed habitats (early seral) would have higher foliar N concentrations than species of mature forests – was largely supported. The four species having the highest foliar N concentrations in our study sites were all forbs that grow commonly in disturbed areas: the natives *Lupinus argenteus*, *Solidago multiradiata*, and *Epilobium angustifolium*, and the non-native *Lactuca serriola*. Moreover, six of the species commonly associated with old forests (*Mahonia repens*, *Carex geyeri*, *Arnica cordifolia*, *Vaccinium scoparium*, *Spirea betulifolia*, and *Lonicera utahensis*) had lower foliar N concentrations than the four herbs listed above. But there were exceptions to these patterns: foliar N concentration was only intermediate in three other species of disturbed habitats,

Table 4
Total % plant cover, total aboveground biomass, total foliar N, net N mineralization, net NH_4^+, and net NO_3^- 2 years post-fire, in relation to site and fire severity, in lodgepole pine forests of Grand Teton National Park, Wyoming, USA

	Mean plant cover (%)	Mean biomass (kg ha^{-1})	Mean foliar N (kg ha^{-1})	Mean net N mineralization (mg-N kg-soil^{-1} year^{-1})	Mean net NH_4^+ (mg-N kg-soil^{-1} year^{-1})	Mean net NO_3^- (mg-N kg-soil^{-1} year^{-1})
Glade site	20.1 (7.6–33.0)	1122 (446–1619)	22.3 (7.8–33.5)	+9.0 (−9.3 to +26.8)	+1.4 (−10.0 to +15.5)	+7.6 (+0.8 to 16.0)
Moran site	16.3 (7.9–26.3)	542 (629–1073)	10.1 (3.8–18.8)	+3.9 (−23.6 to +24.9)	−9.1 (−34.2 to +11.9)	+13.0 (+7.2 to +24.5)
Crown fire stands	14.3 (7.9–21.6)	551 (172–1300)	10.5 (3.8–25.5)	+8.9 (−23.6 to +26.8)	−5.0 (−34.2 to +15.5)	+13.9 (+7.2 to +24.5)
Surface fire stands	22.1 (15.0–33.0)	1107 (629–1619)	21.6 (12.6–33.5)	+4.0 (−9.3 to +24.9)	−2.7 (−16.8 to +11.9)	+6.7 (+0.8 to +13.0)

All stands experienced stand-replacing burns in 2000. Biomass and mean foliar N were measured for eight stands (three at Glade, five at Moran; five crown fire, three surface fire); net N mineralization, net NH_4^+, and net NO_3^- were measured in 10 stands (five each at Glade and Moran; five each in crown and surface burn). Numbers represent means with range (min–max) in parentheses; samples are individual stand means, i.e., $n = 8$ or 10, depending on the variable. None of the apparent differences between the Glade and Moran sites were significant ($P < 0.05$).

Ceanothus velutinus, *Carex rossii*, and *Achillea millefolium*; and the lowest foliar N was in *Calamagrostis rubescens*, a species which may be common in either young or old forests.

Foliar N concentrations in the species we examined were generally consistent with values reported in the literature, although that literature is sparse. Dyrness and Norum (1983) measured N concentrations of 2.4–2.5% in aboveground tissues of *Epilobium angustifolium* in recently burned sites, which is very similar to what we found in our study. Somewhat higher concentrations (ca. 3%) were found in this species grown in pots of natural soil from a site in Holland (van Andel and Vera, 1977). *Epilobium angustifolium* is commonly regarded as a high-nitrogen species, and as an indicator of N-rich sites (e.g., Brakenhielm and Liu, 1998; Frey et al., 2003; but see Bennett et al., 2004), and our findings were consistent with this generalization. *Achillea millefolium*, grown with N-fixers and other native plants present in natural soils in Minnesota, had a foliar N concentration of ca. 2%, similar to our findings (Lee et al., 2003). For *Lactuca serriola*, Jackson et al. (2002) reported mean foliar N of 3.18% in a growth chamber experiment with mycorrhyzae present—a value comparable to our results. We found no reports of foliar N concentrations for any of the other species in our study.

4.2. Question 2. Do foliar N concentrations differ between burned and unburned forests?

We generally supported our prediction that, for a given species, foliar N concentration would be higher in burned areas than in nearby unburned areas (Table 2). Foliar N concentration was significantly higher in burned than unburned stands for three of six species (*Arnica cordifolia*, *Carex geyeri*, and *Vaccinium scoparium*). In no case did we see lower foliar N in the burned area. What was perhaps most interesting was that the three species having significantly higher foliar N in the burned areas were all relatively slow-growing species that typically achieve maximum abundance in late seral forests where N availability is thought to be low. Thus, the higher foliar N concentrations in these three species probably represent luxury consumption, i.e., uptake of N in excess of immediate growth needs (Chapin, 1980). In contrast, the early seral species, with relatively high foliar N but no difference between burned and unburned areas, probably were utilizing the N available to them to support rapid growth.

4.3. Question 3. Do total aboveground biomass, total foliar N, and foliar N content by species differ by site, soil nitrogen availability, or fire severity?

Five of the seven species common in both the Glade and Moran sites exhibited no significant differences in foliar N concentrations between the sites (Table 3). The Glade site appeared to support greater mean biomass and total foliar N than the Moran site (Table 4) – contrary to our prediction that biomass would be greater in the Moran site which had higher total soil nutrient concentrations (Table 1) – but the differences were not significant. Our results appeared to support our

predictions that biomass and total foliar N would be greater in the stands burned by surface fire than in stands with crown fire (Table 4) – though again the differences were not significant. We mention these statistically non-significant patterns only because our small sample sizes and high variances may have obscured genuine patterns of ecological interest. The apparent difference between stands in areas of surface fire and areas of crown fire, if real, probably is related to greater mortality of plants in the crown fire, and the fact that only 2 years had elapsed since the fire.

The N that accumulated in the resin bags over the course of a year was predominantly NO_3^- in both sites. The net N mineralization rates that we measured in this study (mean 9.0 and 3.9 mg-N kg-soil^{-1} year^{-1} at Glade and Moran, respectively, Table 4) were similar to or slightly higher than mean rates measured in a similar-appearing 2-year old stand in Yellowstone National Park (4 mg-N kg-soil^{-1} year^{-1}) (Romme and Turner, 2004). Positive net N mineralization at the Glade and Moran sites resulted from negative or slightly positive net ammonification but strongly positive net nitrification, also similar to the Yellowstone site. In contrast, in an old forest (>300 years) in Yellowstone, net ammonification was substantially higher than net nitrification, and net N mineralization also was higher (13 mg-N kg-soil^{-1} year^{-1}) than in the 2-year old burned stands in Yellowstone or in the present study (Romme and Turner, 2004).

Why were relationships between inorganic N availability (as measured by net N mineralization over the course of a year) and biomass or foliar N so weak or even nonexistent? We suggest four possible interpretations. First, although inorganic N is commonly thought to limit growth in subalpine ecosystems, another nutrient (perhaps phosphorus) may be more important in this early post-fire environment. Moreover, there is evidence that organic N may be a significant N source for vascular plants, especially in low-N ecosystems (Schimel and Bennett, 2004). A second possible reason for weak relationships between N mineralization and plant responses at the stand level is that our in situ resin core method of measuring N mineralization may not provide an accurate estimate of actual inorganic N availability (Schimel and Bennett, 2004). For example, fine roots may grow into the resin bags and directly absorb N (though such roots were not conspicuous in our samples). Moreover, there may have been a residual supply of inorganic N in the soil that was produced by direct pyrolysis of organic matter during the fire, some or much of which had been taken up by residual plants during the first year after the fire (before we installed our resin cores).

A third possible explanation for weak relationships at the stand level is that we simply may have measured N mineralization and plant biomass at the wrong spatial scale (Jenerette and Wu, 2004). In a companion study (unpublished data) we have found substantial spatial structure in net N mineralization at scales <5 m in our stands. A similar study in burned black spruce forest in Alaska reported similar spatial structure in N mineralization and in controlling variables at a range of scales from <1 to >8 m (Smithwick et al., 2005). Thus, even though we characterized both plant cover and net N

mineralization with reasonable sampling adequacy for a given 0.25 ha stand, we may have missed very fine-scale relationships because the vegetation and N mineralization samples were not directly superimposed upon one another.

The fourth possible explanation for the weak relationships between N mineralization and plant responses at the stand level is that the plant community simply has not yet recovered enough total biomass to take advantage of the greater N availability that may exist in some stands. Although we described two classes of fire severity (crown fire and surface fire), both classes were severe enough to have caused significant mortality of the plant community—even among relatively fire-tolerant species having deep roots and other below-ground structures that are insulated by the soil and are capable of re-sprouting after fire (e.g., *Epilobium angustifolium*, *Lupinus argenteus*, *Carex rossii*, and *Calamagrostis rubescens*). More-over, post-fire seedling recruitment in all species was still very limited at this time. Among the 10 stands that we studied, mean plant cover 2 years post-fire was only 18%, and cover in individual stands ranged from as low as 7.6% to a maximum of 33.0%. By comparison, mean cover in four unburned stands (two at Glade, two at Moran) was 48% (range 33–65%).

Overall, our results indicate that plant growth and biomass accumulation are occurring in the second year following natural stand-replacing fire in the Rocky Mountain coniferous forests that we studied. This growth apparently is supported in part by adequate N availability (along with adequate light and water, as well as the biological characteristics of the dominant species). Most of the plants appear to be using the available N for growth, although at least three species (all typical of older forests) seem to be exhibiting luxury consumption of N. A major uncertainty is the source of the available N. It apparently is not coming solely (and perhaps not even primarily) from mineralization of soil organic matter—at least not at the spatial scale at which we measured it. The plants may still be utilizing NH_4^+ that was produced directly through pyrolysis, which we would not have been able to distinguish from NH_4^+ produced via mineralization, or may be using organic N, which was not measured in this study. Moreover, all of these potential N sources may be highly variable and may exhibit significant spatial structure at multiple scales, as has been documented for N mineralization. Our ongoing studies of early post-fire N dynamics in Rocky Mountain subalpine forests are focusing on characterizing spatial structure at multiple scales, and on evaluating the relative importance of various sources of N and of other potentially limiting nutrients.

5. Conclusions

We measured net N mineralization and plant responses (foliar N concentrations and total biomass) in 10 stands representing a range of local soil conditions, pre-fire community composition and structure, and fire severity, 2 years after natural stand-replacing fires in the Rocky Mountains, USA. We documented striking differences in foliar N concentration among the dominant post-fire species, and also determined that foliar N concentration of several species was elevated in the burned stands when compared with unburned areas nearby. When we scaled up to the stand level, however, relationships among N mineralization, fire severity, and plant responses became generally weak or non-existent. The lack of strong patterns at the stand level (i) may indicate that inorganic N does not limit growth in these systems, (ii) may be due to inherent shortcomings of the in situ incubation method for estimating available N over a full year, (iii) may be an artifact of sampling at a spatial scale more coarse than the scale at which the relevant heterogeneity exists, or (iv) may simply reflect the early stage of community reorganization following high fire-caused mortality, such that total plant biomass is insufficient to respond to any local increases in available inorganic N. Companion studies are underway to evaluate the first three of these possible interpretations. If the latter explanation is correct, we predict that patterns will become stronger as we continue sampling these stands over the next several years.

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