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The effects of fire on soil nitrogen associated with patches of the actinorhizal shrub *Ceanothus cordulatus*

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Abstract

Nitrogen is a limiting resource in many temperate forests and nitrogen-fixing plants are usually limited to the early stages of post-disturbance succession. In fire-dependent Sierra Nevada forests, however, *Ceanothus cordulatus* is relatively abundant even in old-growth forest conditions which are at least partly maintained by fire. We conducted a field experiment to determine if soil beneath Ceanothus patches represent 'resource islands' of available N which persist after fire. Nine plots containing discrete patches of Ceanothus, Arctostaphylos patula (manzanita; chosen as a non N-fixing reference species), and bare forest floor were subjected to either a low-intensity (n = 3) or high-intensity (n = 3) bum treatment, or remained unburned as controls (n = 3). Soil temperatures during the bum were monitored by a network of thermocouples placed at the surface of the mineral soil and at ca. 10 cm depths. Soil samples were collected from the organic horizon, 0-10 cm and 15-25 cm depths within each patch type immediately before burning and 2 days, and 6, and 11 months after. Soil moisture, total C and N, and ammonium and nitrate concentrations were determined in the laboratory. Before the burn, Ceanothus patches were significantly enriched in total and inorganic N in the organic horizon relative to the other patch types. A sharp increase in inorganic N was observed in all patch types and depths immediately following burning, but by 6 months after the burn, *Ceanothus* patches were significantly enriched relative to the surrounding patch types and remained so at months. Resprouting Ceanothus patches will continue to be an important source of a limiting nutrient in this fire-prone ecosystem.

Introduction

Although it comprises almost 80% of the earth's atmosphere, the productivity of most temperate terrestrial ecosystems is limited by nitrogen (N; Stacey et al., 1992). Before plants can use atmospheric N, it must first be fixed, a process that occurs predominantly by symbiotic bacteria in association with higher plants (Baker and Mullin, 1992). In Sierra Nevada forests the most common and important N-fixing plants are various species of the woody shrub Ceanothus that grow in association with the symbiotic N-fixing bacteria *Frankia* (Biker and Mullin, 1992; Conard et al., 1985).

N-fixing plants are commonly restricted to the early stages of post-disturbance forest succession, however, our study area in an old-growth forest in the southern Sierra Nevada mountains of California presents an interesting exception as *C. cordulatus* is the most dominant shrub in the understory (North et al., in press). This situation is likely maintained by periodic ground fires that remove trees from the understory and maintain 1an open canopy (Conard et al., 1985). Because Ceanothus has life history traits that make it well-adapted to fire (e.g., Cronemiller, 1959, Keeley, 1977), fire is usually viewed as having a positive effect on *Ceanothus*. However, fire also adversely impacts *Ceanothus* and may limit its role

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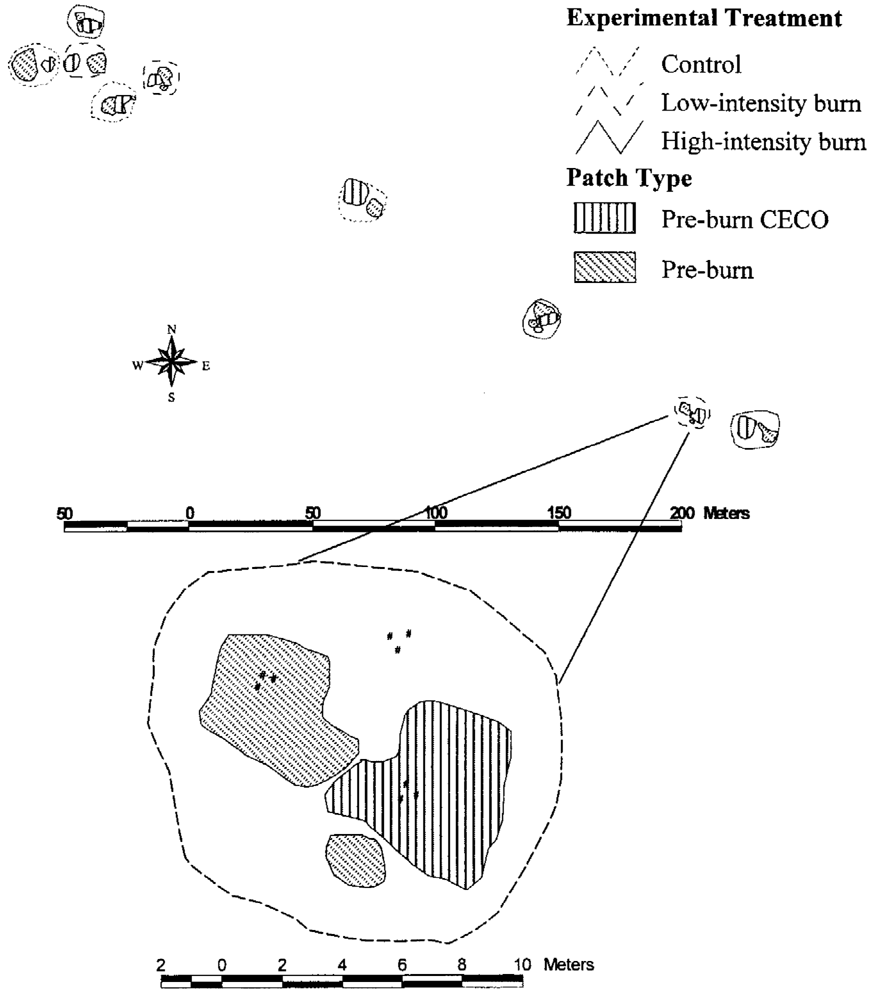

Figure 1. Design and location of experimental burn plots in the field. Soil samples were pooled from the three permanent sampling points shown in the inset to provide one aggregate sample per patch type for each plot. Boundaries around each plot indicate location of fire lines used to prevent fire spread. Fire lines were also established around unburned plots to control for any effects of soil disturbance. Bare forest floor areas are unshaded areas within each patch type.

in forest N accretion. N added to the soil by N-rich *Ceanothus* litter may be lost as fire volatilizes soil N (Woodmansee and Wallach, 1981), and destroys much of the *Ceanothus* and perhaps *Frankia* biomass.

If fire removes a significant portion of the N added to the soil by *Ceanothus*, i.e., eliminates any resource-island effect relative to surrounding areas, then the importance of *Ceanothus* patches to the post-fire N economy may be limited. However, if patches of enriched soil resources associated with *Ceanothus* do persist after fire, then it is likely that these resources are important to the growth of regenerating plants in these N-limited forests. Similarly, fire may limit the importance of the *Frankia–Ceanothus* symbiosis as a source of N by eliminating or significantly reducing *Frankia* in the soil. Previous reports describing distinct taxa of *Frankia* occurring sympatrically (Huguet et al., 2001; Murry et al., 1997; Nalin et al., 1997) suggest the potential for direct or indirect effects of fire to act as a selective force for particular *Frankia* strains. If this is the case, multiple strains of *Frankia* at a single site may contribute to the maintenance of an important ecosystem function following fire.

The current study is the first in a series of experiments designed to address the ecological importance of the *Ceanothus–Frankia* symbiosis in Sierra Nevada forests. As fire is increasingly used as a management tool in the western U.S., it is important to understand the full range of its effects. Future work will more fully examine the effects of fire on *Frankia* and the effects of any post-fire N legacy on establishment and growth of tree seedlings. Although some N is undoubtedly lost during fire, if former patches of *Ceanothus* remain enriched in N relative to their surroundings, this legacy may have important consequences for post-fire forest regeneration. In this study we had two primary objectives. We first measured N in *Ceanothus* patches relative to other dominant understory patch types, and second, quantified the effects of fire on *Ceanothus* and on soil N availability following experimental burning.

Materials and methods

Study area

The 1300-ha Teakettle Experimental Forest is located on the Kings River Ranger District of the Sierra National Forest, approximately 80 km east of Fresno, California. Teakettle climatic conditions are typical of the Mediterranean climate of the west side of the Sierra Nevada mountain range with hot, dry summers and mild, moist winters. Most of the mean annual precipitation of 112 cm yr^{-1} (Berg, 1990) falls as snow between November and May and accumulations of snow generally persist until late May to early June. Teakettle ranges in elevation from 1880 to 2485 m and consists primarily of old-growth, mixed-conifer and *Abies magnifica* (red fir) forests commonly found at middle elevations on the western slopes of the Sierra Nevada (North et al., in press). Soils in the study area are Xeropsamments and Xerochrepts formed from granitic parent materials (Giger and Schmitt, 1993).

Experimental design and plot establishment

Nine experimental plots containing discrete patches of *C. cordulatus*, *Arctostaphylos patula* and bare forest floor were located within 0.25 km of each other along a ridge in Teakettle previously identified as a homogeneous open-canopy forest type (North et al., in press) at ca. 2000 m elevation. *Arctostaphylos* was chosen as one of the most common shrubs within the Teakettle Forest (*Ceanothus* is the most common) and as a non-N-fixing reference species which appears to fill an ecological niche similar to *Ceanothus* (North et al., in press). Plots were approximately 10 × 10 m and received either a low or high-intensity burn treatment. The high-intensity burn treatment was created by adding identical quantities and types of fine woody fuels to each plot, while low-intensity plots were burned with existing fuel loads. Each treatment had three replicates for a total of nine plots including controls. Prior to burning, plot boundaries, three permanent sample points within each patch type, and the perimeter of each shrub patch were mapped (Figure 1) using a Criterion 400 survey laser (LTI, Denver, CO). In November 1999 the burn treatments were applied to these plots and in July 2001, plots were re-mapped and data entered into a Geographic Information System (ArcView; ESRI, Redlands, CA) to quantify the direct effects of fire On aboveground shrub biomass.

To quantify the duration and intensity of soil heating, three soil temperature sensors were placed at the surface of the mineral soil and three at ca. 10-cm depths within each patch type of the six burn plofs. Soil temperatures were recorded at 30-mm intervals for up to days following burning.

Soil N sampling and analysis

Within each plot, soil samples were pooled from the three permanent sample points within each patch type (*Ceanothus*, *Arctostaphylos*, and bare forest floor). Three depths (organic horizon, 0–10 and 15–25 cm) were sampled at each point for a total of nine soil samples per plot. Soil sampling was conducted times: prior to burning in November 1999, 2 days after burning, May 2000, and October 2000. For all sampling dates, soil samples were placed on ice in the field and transported to the lab within 48 h.

Total C and total N concentrations were determined using a Perkin-Elmer CHN Autoanalyzer (model 2400). Ammonium and nitrate concentrations were determined by colorimetric analysis after extraction from soil samples with 2 N KCI (Page et al., 1982). ANOVA with LSD post-hoc analysis was used to compare patch types and treatments.

Results

Pre-burn soil N status

Prior to burning, soil beneath *Ceanothus* patches had significantly more total N, lower C:N ratios, and more inorganic N than the other two patch types. The litter layer of *Ceanothus* patches was significantly ($p = 0.00$) enriched in total N relative to the other patch types and the mean C:N ratio of *Ceanothus* litter (27.4)

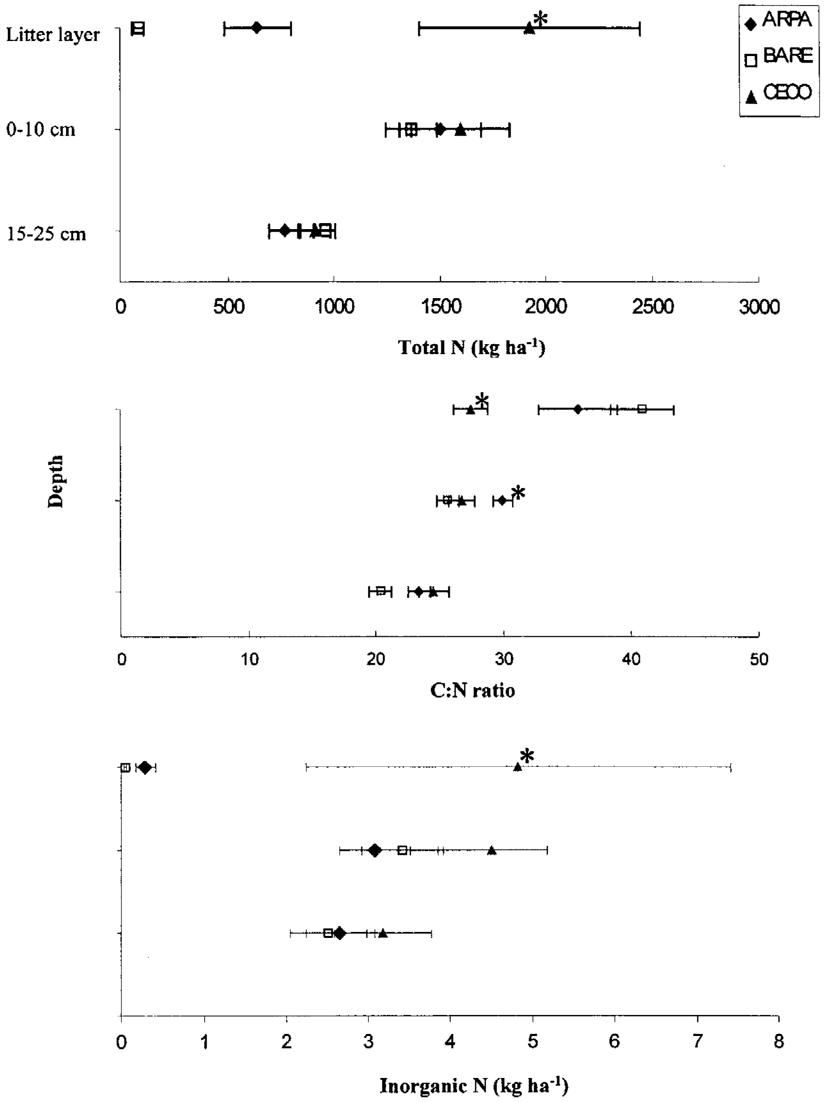

Figure 2. Pre-burn total N pools, C:N ratio, and inorganic N for each patch type and depth. Data points represent means ± 1 standard error. Asterisks indicate significant differences among patch types.

was also significantly lower than that of the *Arctostaphylos* ($p = 0.02$) and the bare ($p = 0.00$) patch types (Figure 2). In the upper level of the mineral soil, the C:N ratio of the *Arctostaphylos* was significantly higher than the *Ceanothus* ($p = 0.02$) or bare patches ($p = 0.00$). The amount of inorganic N in litter beneath *Ceanothus* was also significantly higher than the *Arctostaphylos* ($p = 0.04$) or bare ($p = 0.03$) patch types (Figure 2).

Direct effects of fire

Burn intensity in plots with added fuel was greater than in plots burned with existing fuel loads in terms of both magnitude and duration of soil heating. Mean temperatures at the soil surface were about 1.5–4 times greater in the high intensity burn plots than the low intensity plots and 2–6 times greater below the surface (Figure 3). *Ceanothus* patches in the low-intensity plots experienced only brief surface heating and virtually no sub-surface heating (Figure 3). For both soil depths and burn treatments, *Arctostaphylos* patches experienced greater soil heating than the *Ceanothus* or bare patches. Only in the *Arctostaphylos* plots did the mean maximum subsurface temperature exceed 150 °C (Figure 3).

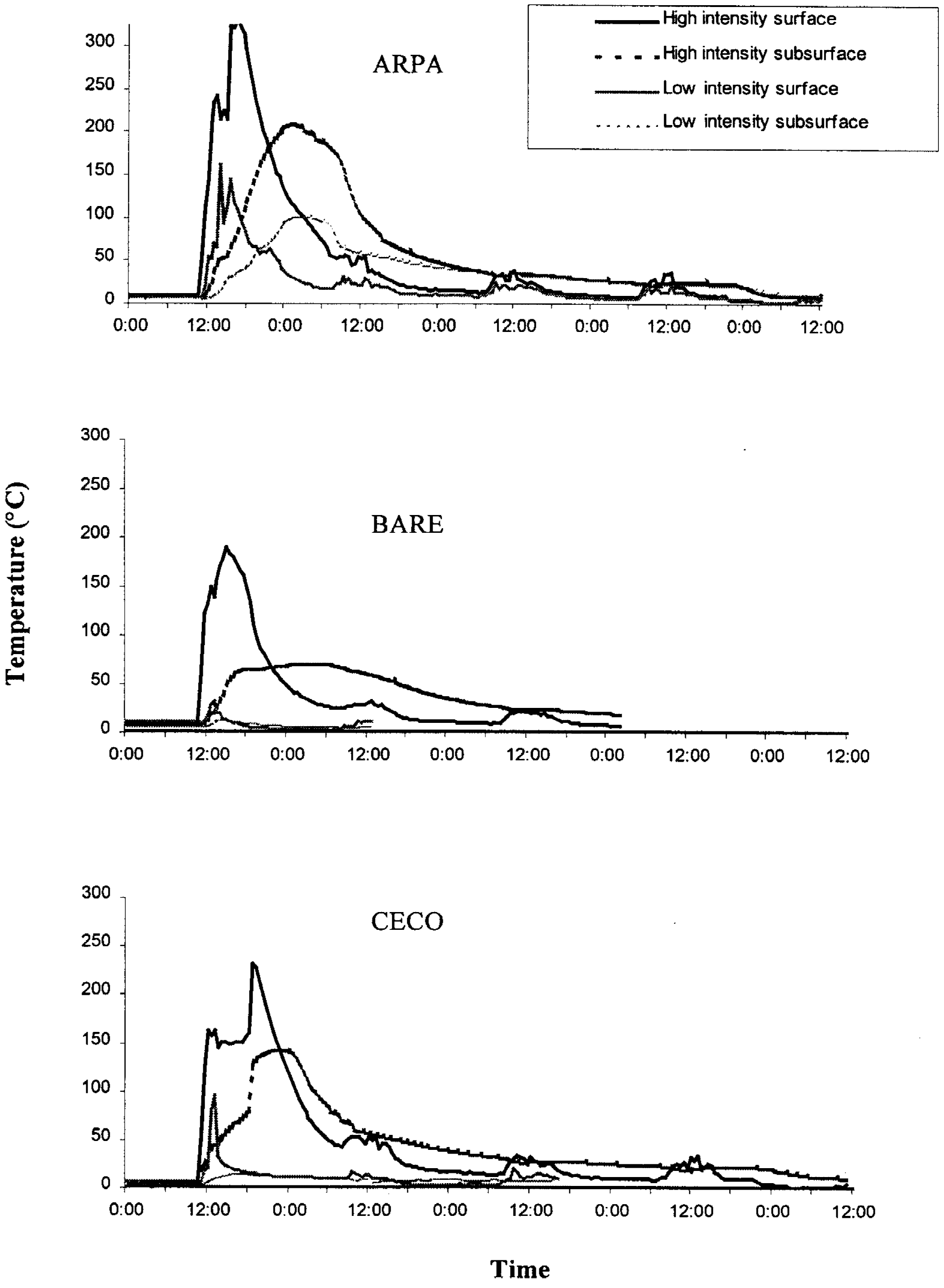

Figure 3. Soil temperature profiles-for high and low intensity bums as measured by surface and sub-surface temperature probes in all three patch types. Depth of sub-surface probes ranged from 7 to 11 cm. For each depth, data represent means from all sensors within the three patches of 1each fuel addition treatment.

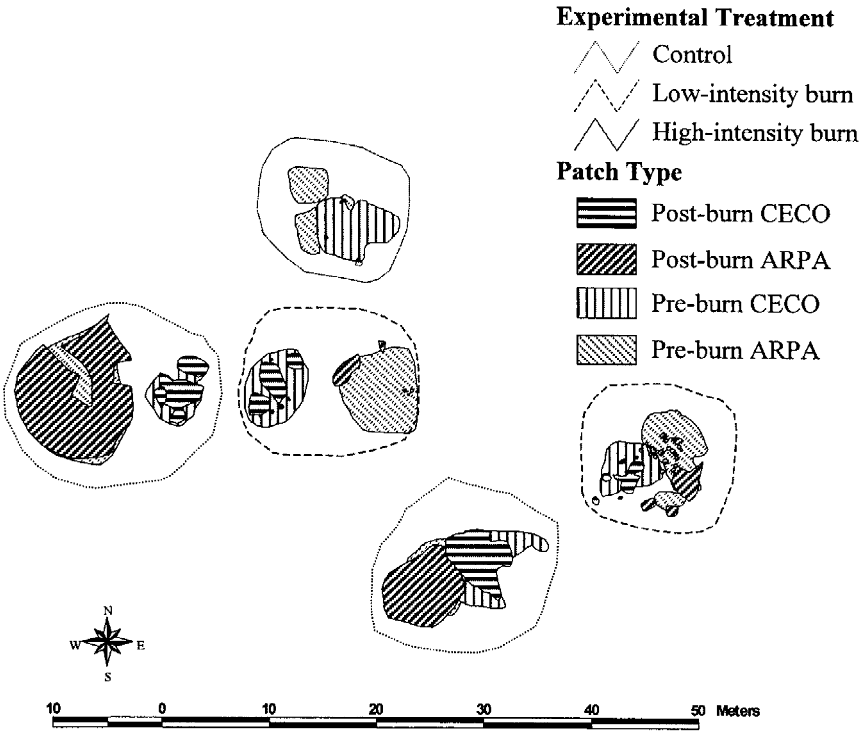

Figure 4. Patch perimeters and locations 18 months after burning compared to pre-burn condition. For clarity, the map excludes the four more distant plots shown in Figure 1.

Table 1. Percent litter consumption and percent reduction in the sum of total shrub cover (m^2) for each patch type and burn intensity. Litter consumption values for the high intensity plots are significantly higher than low intensity plots for all patch types ($p < 0.05$)

Burn Intensity		ARPA		BARE		CECO	
		Mean	SE	Mean	SE	Mean	SE
Control ($n = 3$)	Litter consumption (%)	0	0	0	0	0	0
	Cover reduction (%)	–0.3	–	–	–	6.9	–
Low ($n = 3$)	Litter consumption (%)	38.3	7.3	6.7	3.5	61.1	7.3
	Cover reduction (%)	82.7	–	–	–	73.4	–
High ($n = 3$)	Litter consumption (%)	78.9	6.8	73.3	12.0	86.6	5.9
	Cover reduction (%)	97.5	–	–	–	92.4	–

Litter consumption in the high intensity plots was significantly higher than in the low intensity plots for *Arctostaphylos* ($p = 0.02$), bare ($p = 0.01$), and *Ceanothus* patches ($p = 0.05$; Table 1).

Shrub cover was dramatically reduced due to almost complete combustion of above-ground plant biomass, particularly on the high-intensity burn plots (Table 1, Figure 4). *Arctostaphylos* cover was reduced by 97.5% and *Ceanothus* by 92.4% on the high-intensity plots and 82.7 and 73.4% respectively, on the low-intensity plots (Table 1). Effects of fire on below-ground plant biomass appeared to be much less severe – by the first growing season following burning and into July of the second season, virtually all new growth was due to resprouting, presumably from rootstock that survived the fire. Only six *Arctostaphylos* and nine *Ceanothus* seedlings were found, all of which were on the high-intensity burn plots.

Table 2. Percent moisture content for pre and post-bum soil samples. Autunm post-burn data represent combined means from 1999 and 2000

Depth	Sampling Date	ARPA		BARE		CECO	
		Mean	SE	Mean	SE	Mean	SE
Litter/ash layer	Autumn pre-burn	9.7	0.8	6.6	1.0	13.5	1.6
	Autumn post-burn						
	Control	7.6	2.2	5.9	1.3	10.7	0.7
	Low intensity burn	4.8	1.7	4.4	0.4	4.8	0.8
	High intensity burn	4.1	1.1	4.3	1.5	2.8	1.2
	Spring post-burn						
	Control	12.1	4.2	8.5	1.6	31.7	10.6
	Low intensity burn	9.2	4.2	7.3	1.5	7.0	1.2
	High intensity burn	5.4	0.3	9.4	1.1	8.6	2.3
0–10	Autumn pre-burn	3.9	0.5	2.4	0.4	5.8	0.4
	Autumn post-burn						
	Control	3.3	0.5	2.8	0.8	5.1	0.6
	Low intensity burn	2.7	0.5	1.7	0.5	5.3	1.2
	High intensity burn	3.2	0.9	2.6	1.0	3.1	1.3
	Spring post-burn						
	Control	23.4	4.0	15.3	1.6	25.0	1.5
	Low intensity burn	14.8	2.4	11.5	0.9	23.9	2.7
	High intensity burn	13.3	2.9	15.7	1.9	12.8	4.1
15–25 cm	Autumn pre-burn	3.5	0.3	3.3	0.4	4.3	0.3
	Autumn post-burn						
	Control	3.2	0.3	3.7	0.4	4.2	0.3
	Low intensity burn	4.0	0.5	3.1	0.5	5.0	0.2
	High intensity burn	4.6	0.7	4.2	1.1	5.0	0.7
	Spring post-burn						
	Control	18.1	1.5	15.1	0.1	16.7	1.7
	Low intensity burn	14.9	0.7	13.8	0.4	17.7	1.0
	High intensity burn	14.7	2.0	14.7	1.2	12.5	2.9

Table 3. Host species and elevations of field-collected nodules

Section	Host species	Elevation range of samples (m)	Number of plants sampled
Cerastes	*C.cuneatus*	500–1303	4
Ceanothus	*C. leucodermis*	915–1137	3
Ceanothus	*C. integerrimus*	1768–1811	2
Ceanothus	*C. parvifolius*	1768–1931	
Ceanothus	*C. cordulatus*	1885–2045	6

Prior to burning, soil moisture of the organic horizon and 0–10 cm depth of the mineral soil within *Ceanothus* patches was higher than the other two patch types, but moisture differences among the patch types following burning were generally not significant (Table 2).

Effects of fire on soil N status

Total N

For all patch types, total N pools in the organic horizon were reduced in the burned plots, but the effect of burn intensity was not significant. In the low-intensity burn plots, *Ceanothus* patches remained enriched in total N. Total N following fire in the *Ceanothus* ash

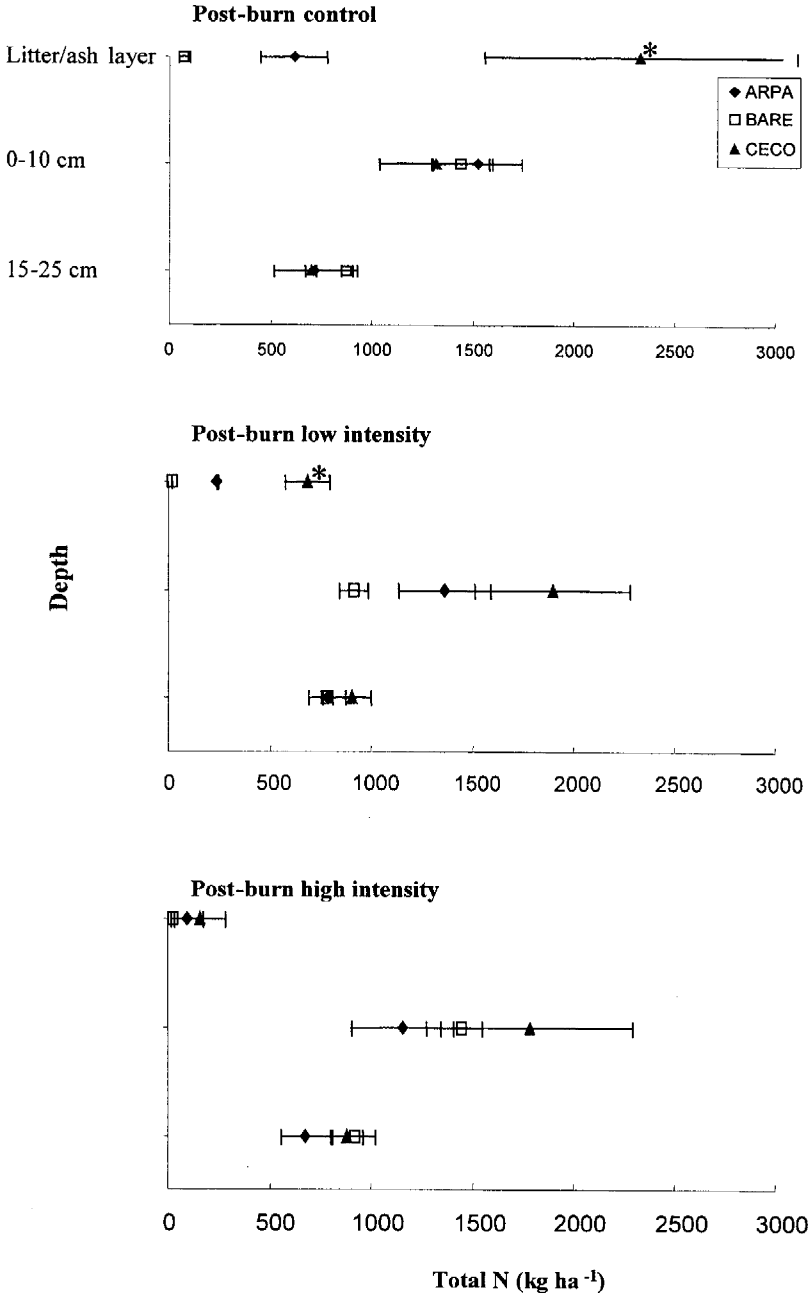

Figure 5. Total N pools 2 days following burning for both burn treatments and controls. Data points are means ± 1 standard error. Asterisks indicate significant differences among patch types.

layer in the low-intensity plots was significantly higher than the *Arctostaphylos* (p = 0.00) or bare (p = 0.00) patches (Figure 5). Total N amounts in the high-intensity plots were not significantly different by patch type (Figure 5).

C:N Ratio

Following burning, the C:N ratio in *Ceanothus* patches generally remained lower than the other two patch types (Figure 6). In the high-intensity burn plots, the C:N ratio in *Ceanothus* patches was significantly lower than the *Arctostaphylos* or bare patches in the

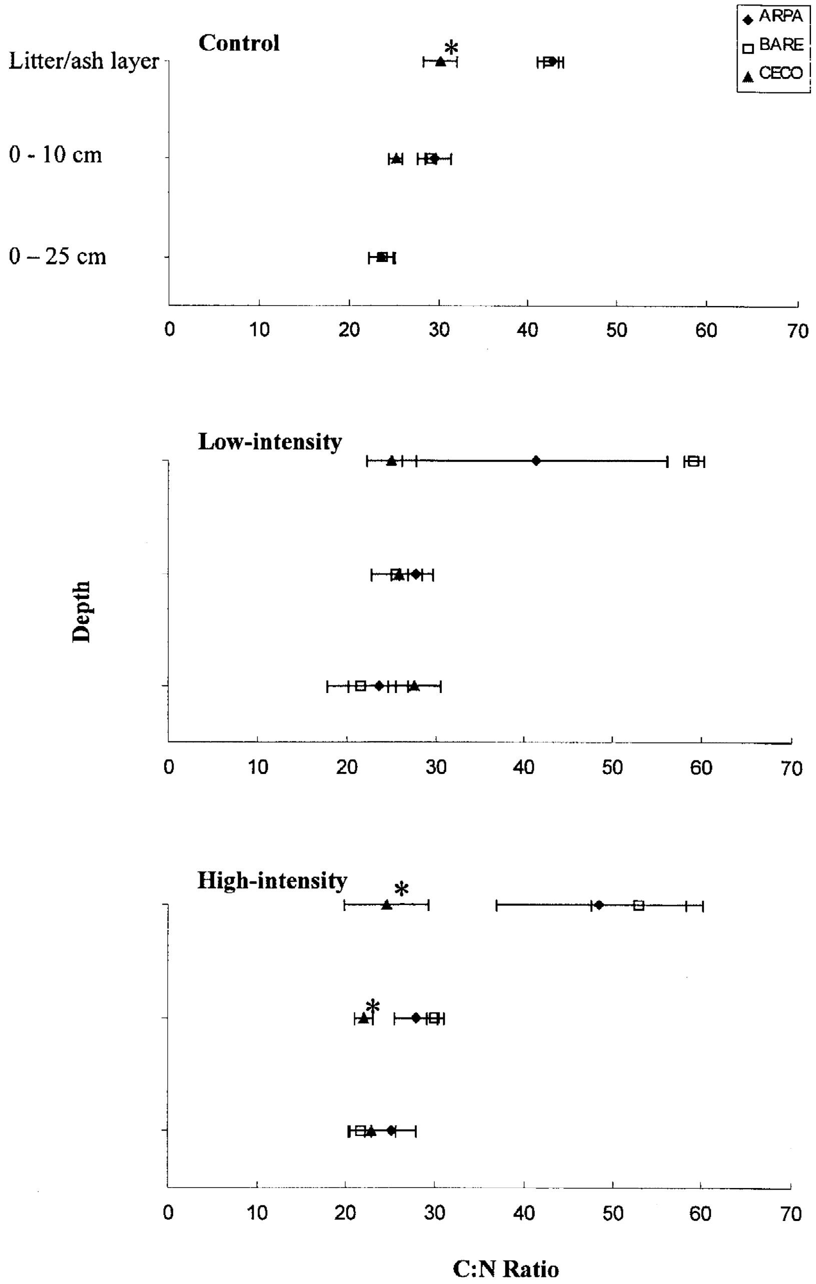

Figure 6. C:N ratios for each patch type and depth following burning. Data points are means ± 1 standard error. Asterisks indicate significant differences among patch types.

organic horizon ($p = 0.05, 0.04$ respectively) and the mineral soil ($p = 0.04, 0.01$; Figure 6).

Inorganic N

Immediately after burning, inorganic N levels increased dramatically in all patch types particularly in the high-intensity bum plots (Figure 7). At 6 and momths after burning, inorganic N levels were still elevated relative to pre-burn levels, but had fallen by up to 10× from immediately after the fire and were relatively consistent between the latter two sampling dates (Figure 7).

Ceanothus patches generally remained enriched in inorganic N following fire (Figure 7). Relative to the

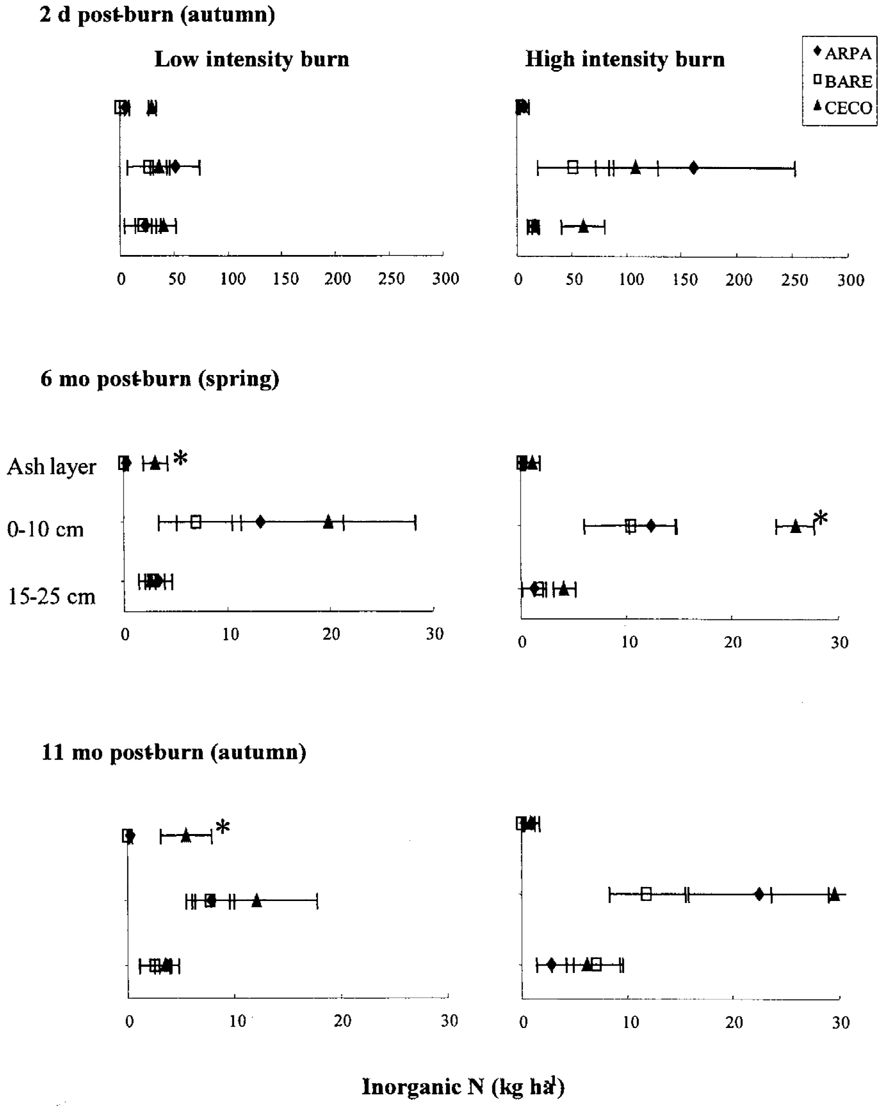

Figure 7. Inorganic N amounts for low-intensity and high-intensity burn plots 2 days and 6 and 11 months after experimental burning. Note *X*-axis scale for upper two figures is 10× that of the lower figures. Data points represent means ± 1 standard error. Asterisks indicate significant differences among patch types.

Arctostaphylos and bare patches, *Ceanothus* patches had significantly more inorganic N in the ash layer of the low intensity plots at 6 months ($p = 0.03, 0.02$, respectively) and 11 months ($p = 0.04, 0.03$) after burning, and in the 0–10 cm depth of the mineral soil of the high intensity plots at 6 months after burning ($p = 0.02, 0.01$; Figure 7).

Discussion

Prior to burning, soils underneath *Ceanothus* patches were generally enriched in total and available forms of N and had lower C:N ratios relative to other patch types common in mixed-conifer forests. *Ceanothus* patches can be considered resource islands in these forests, although nitrogen enrichment was most pronounced in the litter layer and decreased in the 0–10 and 15–25 cm depths of the soil. Whether the increased N availability in *Ceanothus* patches actually translates to increased tree growth may have important management implications. The current study is intended as a building block for ongoing work investigating whether *Ceanothus* patches facilitate conifer establishment or growth. *Ceanothus* in other western forest ecosystems has been shown to be an important source of N (Binkley and Husted, 1982; Conard et al., 1985; Youngberg et al., 1979), but many questions remain about its functional importance. Shrub patches in mixed conifer may play an important role in succession if they provide a more favorable micro-climate or nutrient-rich microsites in the harsh growing conditions of the southern Sierra Nevada.

Following burning, total N pools in the organic horizon were reduced, largely due to consumption of organic matter and volatilization of N at temperatures above 175–200 °C (Agee, 1993) in the high-intensity burn. However, the effect of burn intensity was not significant and N enrichment of *Ceanothus* patches persisted throughout the course of the study. Immediately after the burn there was a large spike in available N in all patch types which is a common short-term result of fire (Christensen, 1994; Woodmansee and Wallach, 1981). After the initial pulse, *Ceanothus* patches in both the low- and high-intensity bum plots were again generally enriched in available forms of N relative to the other patch types at 6 and months after burning. This trend is likely to continue – only in the *Ceanothus* patches were C:N ratios below 30 (the point at which net N mineralization generally occurs; Perry, 1994) before and after burning. Higher soil moisture content in *Ceanothus* patches may also contribute to increased N mineralization.

If *Ceanothus* does continue to have more available N than the other patch types, this long-term effect may be particularly important for tree seedling growth. Fire removes most of the above-ground *Ceanothus* biomass, leaving nitrogen-rich, bare mineral soil. Resprouting of *Ceanothus* may compete with tree seedlings, but also provides ongoing N inputs and may ameliorate microclimate. Successful establishment of tree seedlings in the Sierra Nevada has been shown to be primarily limited by microclimate (Delucia et al., 1988; Tappeiner and Helms 1971). not soil nutrient availability. Soil N likely becomes most important for tree seedlings after they have cleared the initial hurdle of establishment. Thus, the long-term importance of *Ceanothus* patches for tree growth may depend on continued availability of N and continued N fixation by *Frankia*.

In this study we were also interested in the effects of fire on *Frankia*. We attempted to measure fire-induced changes in the number and type of *Frankia* forming nodules by using *C. cordulatus* seedlings as trap plants grown in the greenhouse with pre and post-burn soils from our field experiment. Unfortunately, few plants formed nodules in the greenhouse which is consistent with the experience of other researchers using *Ceanothus* as a bioassay for *Frankia* (D.D. Myrold, personal comm.). However, based on two lines of indirect evidence, we inferred that fire is unlikely to reduce the number of *Frankia* in the soil or select for particular strains of *Frankia* nodulating *Ceanothus* at the scale of our experiment.

First, minimal soil heating at depth and vigorous resprouting in the low-intensity burn treatment suggests most Fran/cia likely survived the fire. Soil heating was of greater magnitude and duration in the high-intensity burn treatment, but again, resprouting suggests *Ceanothus* roots, and probably *Frankia* as well, survived. Because most plants are resprouting from surviving root stock even in the high-intensity burn plots and soil heating is extremely variable and greatly reduced by depth, we find it unlikely that burning had a large direct effect on *Frankia* in the soil. Common indirect effects of fire such as higher pH or the creation of hydrophobic layers in the soil (Christensen, 1994; Woodmansee and Wallach, 1981) could also affect *Frankia*, but in our experience most nodules are found below 20 cm deep where these effects are likely minimal.

Second, to indirectly assess the possibility of fire acting as a selective agent for particular strains of *Frankia* in the burn experiment, we collected nodules from host plants representing five species of *Ceanothus* across an elevational gradient of ca. 1500 m (Table 3). Using nodule tissue from each host individual, we amplified and sequenced a 2098 bp portion of *Frankia* DNA that includes the 3′ end of the 16S rRNA gene, the intergenic spacer (IGS), and the 5′ end of the 23S rRNA gene. Initial phylogenetic analysis of Fran/cia diversity at this regional scale indicates two distinct groups that appear to be distinguished by elevation (not shown). Although this work is ongoing, our results to date are consistent with previous research in Oregon in which distinct *Frankia* strains nodulating *Ceanothus* were found at the scale of major biogeographic provinces (Ritchie and Myrold, 1999), and suggest it would be unlikely to find novel *Frankia* strains nodulating *Ceanothus* after a localized disturbance such as the experimental burning described in the current study. Because our sampling was restricted to *Frankia* that formed nodules on *Ceanothus*, it is not inconsistent with previous studies demonstrating distinct taxa of *Frankia* occurring sympatrically (e.g., Huguet et al., 2001; Murry et al., 1997; Nalin et al., 1997), as *Frankia* strains forming nodules on a particular host plant likely represent a subset of *Frankia* that may exist in the soil.

Before 20th century fire suppression, most western coniferous forests experienced frequent, low intensity surface fires. With several decades of fuel accumulation, many forests may now bum at a higher intensity than they would have in the past. This change in the disturbance regime is likely to significantly impact the understory plants of these forest communities. Fuel loads in the high-intensity plots in this study were consistent with local areas of heavy fuel accumulation in fire-suppressed forests and may provide an analog of the effects of fire in these types of forests. Because many of the parameters we measured in this study were not significantly negatively affected by the higher burn is intensity, our results may provide support for re-introducing controlled burning even in fire-suppressed forests.

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