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## Fire effects on ecosystem nitrogen cycling in a Californian bishop pine forest

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**Abstract** Fire can cause severe nitrogen (N) losses from grassland, chaparral, and temperate and boreal forest ecosystems. Paradoxically, soil ammonium levels are markedly increased by fire, resulting in high rates of primary production in re-establishing plant communities. In a manipulative experiment, we examined the influence of wild-fire ash residues on soil, microbial and plant N pools in a recently burned Californian bishop pine (*Pinus muricata* D. Don) forest. Ash stimulated post-fire primary production and ecosystem N retention through direct N inputs from ash to soils, as well as indirect ash effects on soil N availability to plants. These results suggest that redistribution of surface ash after fire by wind or water may cause substantial heterogeneity in soil N availability to plants, and could be an important mechanism contributing to vegetation patchiness in fire-prone ecosystems. In addition, we investigated the impact of fire on ecosystem N cycling by comparing  $^{15}\text{N}$  natural abundance values from recently burned and nearby unburned *P. muricata* forest communities. At the burned site,  $^{15}\text{N}$  natural abundance in recolonising species was similar to that in bulk soil organic matter. By contrast, there was a marked  $^{15}\text{N}$  depletion in the same species relative to the total soil N pool at the unburned site. These results suggest that plant uptake of nitrate (which tends to be strongly depleted in  $^{15}\text{N}$  because of fractionation during nitrification) is low in recently burned forest communities but could be an important component of ecosystem N cycling in mature conifer stands.

**Key words** Ash · Primary production · Natural abundance  $^{15}\text{N}$  · Nitrate · *Pinus muricata*

### Introduction

Fires are a major perturbation of ecosystem nutrient cycling in grasslands, chaparral, and temperate and boreal forests (Kosłowski and Ahlgren 1974). As a result of fire, nutrients accumulated in above-ground biomass and litter are either lost to the atmosphere through combustion, deposited as ash, or retained in incompletely burned organic matter (Boerner 1982). In particular, fire results in substantial ecosystem nitrogen (N) losses through volatilisation and soil leaching (Grier 1975; DeBano and Conrad 1978; Vitousek and Howarth 1991). Paradoxically, despite these losses, soil ammonium ( $\text{NH}_4^+$ ) pools may be increased by up to an order of magnitude in recently burned ecosystems (Christensen and Muller 1975; Raison 1979; Stock and Lewis 1986; Naveh 1990; Wienhold and Klemmedson 1992; Fenn et al. 1993). In addition, plant primary production rates are generally enhanced in recently burned vegetation communities (Kosłowski and Ahlgren 1974; Keeley et al. 1981; Boerner 1982; Tyler 1996). However, the mechanisms by which wildfires enhance soil N availability and primary production are not well understood, despite their importance to the recovery and management of fire-prone ecosystems.

Fire may influence soil N availability through heating effects on soils, ash deposition of N previously contained in vegetation, alteration of soil microclimate by removal of vegetation/litter, and/or changes in microbial N immobilisation resulting from changes in soil C stocks (Raison 1979). Laboratory microcosm experiments indicate that  $\text{NH}_4^+$  pool size in burned soils is positively correlated with soil temperature during fire (Klopatek et al. 1990), suggesting that soil heating is the primary mechanism enhancing N availability immediately after fire. Ash residues are an important pathway of nutrient return from above- to below-ground for phosphates, magnesium, po-

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tassium and calcium (Raison 1979). Although  $\text{NH}_4^+$  content in ash is relatively low (Grier 1975; Raison 1979), considerable organic N may be present in the ash (Christensen and Muller 1975; Grier 1975; Stock and Lewis 1986) suggesting that ash deposits could provide an important source of N after fire (Raison 1979). Furthermore, ash may have indirect effects through increases in soil pH (Raison 1979) that could stimulate N cycling below-ground, enhancing  $\text{NH}_4^+$  pools in burned soils. Many previous studies have addressed the impact of fire on aspects of ecosystem N cycling using comparisons of burned and unburned sites (Christensen and Muller 1975; DeBano and Conrad 1978; Raison 1979; Wienhold and Klemmedson 1992). In an effort to separate and understand the individual mechanisms by which fire alters nutrient availability, Fritze et al. (1994) added ash to unburned forest sites and examined soil carbon and N pool responses. Here, we investigated the effect of natural ash deposition on post-fire ecosystem N cycling by removing the surface ash layer from field plots within 1 week of a wildfire in a Californian bishop pine (*Pinus muricata* D. Don) forest. We characterised the influence of ash on plant, soil and microbial N pools during the first growing season after fire in order to test the hypothesis that ash deposition during wildfires can enhance soil N availability to plants and facilitate ecosystem N retention. In addition, we investigated the impact of fire on source pools for plant N acquisition by contrasting  $^{15}\text{N}$  isotopic natural abundance values in plants and soils from burned and nearby unburned *P. muricata* forest communities.

## Materials and methods

### Study site

This research was conducted in a *P. muricata* forest within the Point Reyes National Seashore in northern California (38°03'39" N, 122°50'24" W, elevation 210 m). The climate is mediterranean with cool, wet winters and warm, dry summers. Soil moisture levels are dominated by rainfall from November through May although coastal fog drip occurs throughout the year. *P. muricata* is a serotinous-coned species that releases its seeds after intense heat, resulting in small even-aged stands (Munz and Keck 1968). These stands tend to develop in the Californian coastal fog belt on ridge tops surrounded by northern coastal scrub communities dominated by coyote bush (*Baccharis pilularis* C.B. Wolf) (Barbour and Major 1988). Before the introduction of fire management practices, wildfire was a regular perturbation of these ecosystems occurring approximately every 40 years (Sugnet 1985). Trunk cross-sections indicated that the trees at the burned site ranged from 32 to 38 years old. For comparison with the burned site, we sampled plants and soil from an unburned, mature forest stand of *P. muricata* in April 1998. The unburned site was similar in size, age and plant community composition to the *P. muricata* stand at the burned site and was located approximately 16 km further north along the Point Reyes coast at Tomales Bay State Park (38°07'54" N, 122°53'32" W).

A major wildfire burned 48 km<sup>2</sup> of the Point Reyes National Seashore during 3–17 October 1995. The fire intensity at our experimental site was severe enough to consume all understory leaf material, the complete surface soil organic layer and to kill all *P. muricata* trees. On 23 October 1995, we established pairs of plots

1–3 m apart in seven blocks located randomly on clear patches of the forest floor along a broad transect covering an area of approximately 20×50 m. Within each block, the plots (1.4×1.4 m) were bordered by wooden frames 15 cm high and assigned randomly to treatment or control. We used a back-pack leaf-blower to remove the surface ash layer (including seed and charcoal material) from the treatment plots. Afterwards, all frames (treatment and control) were immediately covered with black PVC sheeting to prevent wind dispersal of ash into or out of the plots. This sheeting was removed after consolidation of the surrounding surface ash layer by the first substantial rains in late November. The serotinous nature of *P. muricata* cones and the intense heat of the fire resulted in an extensive *P. muricata* seed rain onto the forest floor in the days immediately after the burn. Since the blower treatment removed naturally dispersed *P. muricata* seeds in the ash-removed plots, we planted 100 locally collected *P. muricata* seeds in both treatment and control plots in late November. As a result, the density of *P. muricata* seedlings in the control plots was 2.5 times higher than in the ash-removed plots at the time of harvest. We assume that the blower treatment did not influence establishment of plant species other than *P. muricata* because (1) seed dispersal from species other than overlying *P. muricata* is likely to have been minimal in the few days between the end of the fire and the establishment and covering of the plots, (2) seeds that were present on the soil surface at the site prior to the fire would have been burned and (3) seeds present below the soil surface that survived the fire should have been unaffected by the blower treatment. We assayed post-fire viability in the seedbank to 5-cm soil depth by monitoring seedling germination from soil samples (176 cm<sup>2</sup>,  $n=16$ ) taken randomly across the site at the time of plot establishment. The soils were placed in trays in a glasshouse, moistened regularly and monitored for seedling emergence over the following 2 months. With the exception of two herbs that germinated from one of the soil samples, all emerging seedlings were *P. muricata* indicating that the fire destroyed most seeds that were present in the upper soil horizon prior to the burn.

### Soil, ash and plant nutrient analyses

On 23 October and 4 December 1995, 15 January and 12 March 1996 and close to the end of the first growing season on 15 May 1996, we sampled six soil cores (10 cm depth, 2 cm diameter) randomly from the central 1 m<sup>2</sup> of each plot. In control plots, these cores included the ash layer. On the first sampling date, we also collected ash samples ( $n=10$ ) from the surface of the forest floor using small frames (176 cm<sup>2</sup>). The ash samples were taken from undisturbed areas chosen at random across the site. These samples were sieved (1 mm) and analysed ( $n=3-4$ ) as described for soils. We estimated surface ash deposition (particles <1 mm diameter) at our site as 1237 g m<sup>-2</sup> (SE=226,  $n=10$ ) and bulk densities as 0.528 g cm<sup>-3</sup> (ash), 0.659 g cm<sup>-3</sup> (soil). These data suggest that the average thickness of the ash layer was approximately 2.3 mm.

The soils were sieved (2 mm) to remove stones and coarse roots prior to extraction (within 36 h of sampling). Moisture content was determined by drying sub-samples at 65°C for 48 h. Soil pH was measured in a solution of 5 g fresh soil to 5 ml distilled H<sub>2</sub>O that had been shaken and then allowed to settle for 10 min (McLean 1982). Soil ammonium and nitrate were measured by extracting about 20 g of fresh soil in 50 ml 2 M KCl. The solutions were shaken for 1 h and then filtered (Whatman no. 1) before freezing. The filter paper was pre-leached with about 30 ml of the extracting solution to remove any soluble inorganic N from the paper. Later, samples and blank controls were analysed colorimetrically for  $\text{NH}_4\text{-N}$  (Lachat 1990a) and  $\text{NO}_3\text{-N}$  (Lachat 1989). Soil pH and extractable N content were also measured on 5 April 1997.

Microbial biomass nitrogen (N) and carbon (C) were determined as chloroform-labile N and C by the direct extraction method (Brookes et al. 1985), using soils at field moisture and a 1-day fumigation period (Davidson et al. 1989; Hart et al. 1993). Tests with our soil indicated that a 1-day fumigation period was sufficient to maximise chloroform-labile N release. Soils (about 20 g)

were extracted with 50 ml 0.5 M  $K_2SO_4$ , shaken for 2 h, filtered as above and then frozen. Later, the N present in the extracts was converted to  $NH_4^+$  by micro-Kjeldahl digestion and analysed colorimetrically (Lachat 1992). Since chloroform releases only a fraction of total microbial biomass N, we used a seasonally averaged division factor of 0.25 (Davidson et al. 1989; Hart et al. 1993) to calculate microbial N values from the chloroform-labile N results. Total organic carbon (TOC) content of the extracts was determined on a TOC analyzer (Shimadzu). We used a division factor of 0.35 (Horwarth and Paul 1994) to calculate microbial C from the chloroform fumigation-direct extraction data. Soluble soil organic N was estimated by subtracting total KCl-extractable inorganic N values from the non-fumigated digested  $K_2SO_4$ -extract values. Since we did not correct for any difference in efficiency associated with the different extracting solutions, we have most likely underestimated the soil soluble organic N fraction.

Isotopic  $^{15}N$  ratios in soil, ash and plant samples were determined by isotope ratio-mass spectrometry (IR-MS). The natural abundance of  $^{15}N$  was expressed as  $\delta^{15}N$  (‰) =  $1000(R_{\text{sample}} - R_{\text{standard}}) / R_{\text{standard}}$  where  $R = \text{mass } 29 / \text{mass } 28$  and the atmospheric  $\delta^{15}N = 0$  by definition (Shearer and Kohl 1989). Total N in soil, ash and plant samples was determined by IR-MS and in many cases also by micro-Kjeldahl digestion/colorimetric analyses (Lachat 1990b). Total N results from both methods using the same samples were closely correlated ( $r > 0.88$ ,  $P < 0.001$ ) indicating good methodological precision. Here, we report only the IR-MS data. All below-ground N pools are calculated to a depth of 10 cm and include the ash layer in control plots.

#### Plant production

At the end of the first growing season (15 May 1996), all above-ground vegetation (except *P. muricata*) was harvested from the central 1 m<sup>2</sup> of each plot. *P. muricata* seedlings in each plot were counted before taking a random sub-sample ( $n=4$ ) to estimate total *P. muricata* biomass per plot. Plant species were sorted into groups that most likely established from seed ('herbs' and 'N-fixers') and those that emerged from existing root stock ('resprouters'). Plant identifications are presented at the genus level because the absence of reproductive structures precluded more precise classification of many taxa. All plant material was dried at 65°C for 96 h before determining mass. Above-ground plant N pools for each plant group were estimated using the mean leaf N concentration of two species within each group (indicated in Table 1) that were chosen on criteria of plot frequency and then biomass dominance.

#### Statistical analyses

The effects of treatment on above-ground biomass for the whole community and for each plant group were investigated using paired *t*-tests. In two of the ash-removed plots, shoot biomass was dramatically increased by the presence of *Marah* sp. This species can develop considerable ground-cover after fire through proliferation of annual stems that originate from large tubers persisting at depth (Munz and Keck 1968; Schlising 1969). Stems at our site extended laterally up to 8 m in length across the soil surface. The habit of emergence from deep tubers and extensive stem proliferation make it unlikely that the presence of shoots of this species within a plot reflected local soil conditions. To remove heterogeneity due to this species in an unbiased manner, we excluded the two affected plots from all plant data analyses.

Repeated-measures analyses of variance were used to test for ash effects on soil pH (as mean  $H^+$  ion concentration), microbial biomass N content, and soil ammonium and nitrate pools during the first growing season. The month during which the samples were taken was treated as a categorical variable. Treatment effects on soil and microbial N pools at the end of the first growing season were investigated using paired *t*-tests. Pearson's correlation followed by Bartlett's chi-squared test for significance (Systat 5.2) was used to examine the relationship between above-ground biomass and total N content in the upper 10 cm of the forest floor.

**Table 1** Plant community composition at the end of the first growing season after fire. Data are shown as mean (SE in parentheses) above-ground biomass of each species per plot (g m<sup>-2</sup>),  $n=7$  (control),  $n=5$  (ash removed). Different superscript letters for the total means indicate a significant difference at  $P < 0.05$ . Species with asterisks were analysed for tissue N content

	Above-ground biomass (g m <sup>-2</sup> )	
	Control	Ash-removed
<b>Herbs</b>		
<i>Stachys</i> sp.*	10.9 (4.4)	2.4 (1.7)
<i>Convolvulus</i> sp.*	8.3 (4.7)	0.2 (0.2)
<i>Geranium</i> sp.	2.8 (2.8)	5.0 (3.1)
<i>Cirsium</i> sp.	1.6 (1.6)	–
<i>Montia</i> sp.	1.3 (1.3)	–
Unidentified A	1.3 (1.1)	–
Graminoids	0.3 (0.2)	–
Unidentified C	–	1.9 (1.9)
<i>Senecio</i> sp.	–	0.7 (0.7)
<b>N-fixers</b>		
<i>Lotus</i> sp.*	5.4 (2.6)	4.9 (2.7)
<i>Trifolium</i> sp.	2.4 (0.9)	5.1 (2.2)
<i>Ceanothus thyrsiflorus</i> *	1.7 (1.1)	3.8 (1.5)
<i>Vicia</i> sp.	0.1 (0.1)	–
<i>Lupinus</i> sp.	–	0.2 (0.2)
Unidentified B	0.1 (0.1)	–
<b>Resprouters</b>		
<i>Rubus</i> sp.*	43.1 (15.6)	10.5 (6.7)
<i>Pteridium aquilinum</i> *	35.5 (12.3)	5.9 (3.8)
<i>Lonicera</i> sp.	3.3 (3.3)	–
<i>Toxicodendron diversilobum</i>	1.1 (0.7)	–
<i>Pinus muricata</i>	3.2 (0.6)	1.3 (0.3)
Mean total above-ground biomass per plot	122.3 <sup>a</sup> (24.0)	41.8 <sup>b</sup> (11.9)

## Results

Ash significantly enhanced total above-ground primary production during the first growing season after fire (Table 1). The distribution of biomass between 'herb', 'N-fixers' and 'resprouter' plant groups was similar in plots from which ash was removed (Fig. 1). However, those species that can resprout after fire were stimulated in the presence of ash, leading to their marked dominance in the post-fire plant community of control plots (Table 1, Fig. 1).

Treatment effects on soil and plant N pools strongly suggest that ash stimulated primary production by enhancing soil N availability to plants. First, the presence of surface ash significantly increased total below-ground Kjeldahl-digestible N to 10 cm depth (Table 2). Second, shoot biomass across treatment and control plots was closely correlated with total below-ground N (Fig. 2), suggesting that primary production was limited by N supply even in the first growing season after fire. Furthermore, shoot N in the plant community was significantly enhanced by ash (Table 2) in a pattern similar to the stimulation of primary production (Fig. 1). Finally, the presence of ash resulted in a strong trend towards increased soil  $NH_4^+$  pools from early December through to

**Table 2** Ecosystem N pools at the end of the first growing season after fire ( $\text{g N m}^{-2}$ ). Below-ground N pools are calculated to 10 cm depth in the forest floor and include the surface ash layer in control plots ( $n=7$ , mean with SE in parentheses). Means within a row that are followed by a different superscript letter indicate sig-

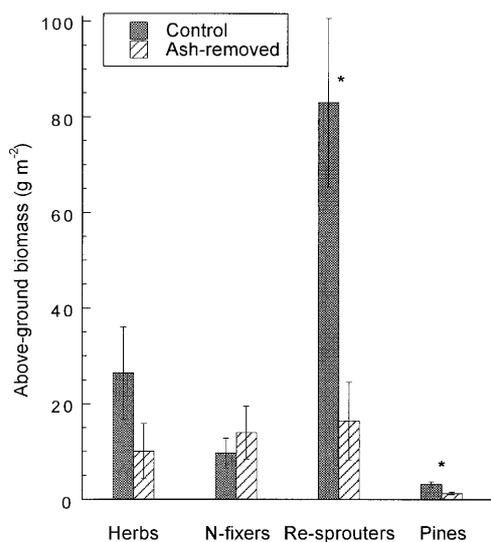
nificant paired  $t$ -test differences:  $^b P < 0.05$ ,  $^c P < 0.01$ . N pools in surface ash sampled immediately after the fire are also shown ( $n=3-4$ ). Total N measurements below-ground include microbial N, inorganic N, soluble and insoluble organic N, but not N contained in roots

	Control plots	Ash-removed plots	Surface ash
Above-ground			
Shoot N	3.2 <sup>a</sup> (0.6)	1.3 <sup>b</sup> (0.3)	
Below-ground			
Microbial N	4.6 <sup>a</sup> (0.7)	3.8 <sup>a</sup> (0.7)	
Extractable $\text{NH}_4^+$ -N	0.8 <sup>a</sup> (0.2)	0.8 <sup>a</sup> (0.1)	0.2 (0.03)
Extractable $\text{NO}_3^-$ -N	0.3 <sup>a</sup> (0.1)	0.4 <sup>a</sup> (0.1)	0.01 (0.002)
Soluble organic N	0.5 <sup>a</sup> (0.1)	0.6 <sup>a</sup> (0.1)	Not measured
Total N (Kjeldahl)	150.9 <sup>a</sup> (11.4)	125.1 <sup>c</sup> (12.0)	8.9 (0.3)
Root N	Not measured	Not measured	

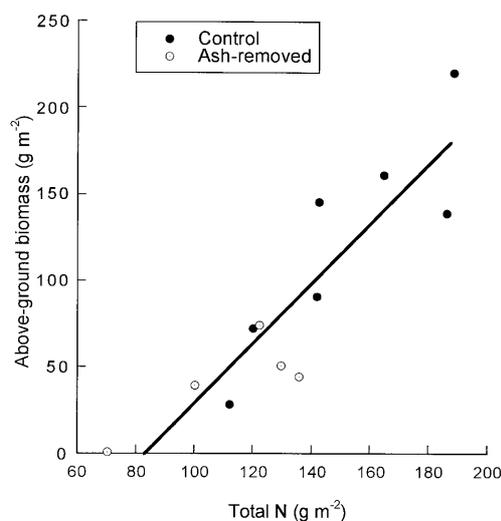
**Table 3** Repeated-measures statistical analyses of soil  $\text{NH}_4^+$ -N,  $\text{NO}_3^-$ -N, microbial N and soil pH over the first growing season after fire ( $n=6-7$ , except microbial N data for December where

$n=4$ ). Block could not be included in the analysis of microbial N because of missing values. Significant  $P$ -values are *italicised*

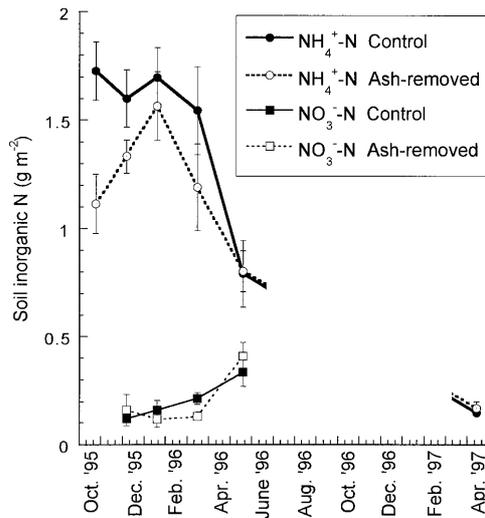
	Soil $\text{NH}_4^+$ -N (December–March 1996)			Soil $\text{NO}_3^-$ -N (December–May 1996)			Microbial N (December–May 1996)			Soil pH (December–May 1996)		
	<i>df</i>	<i>F</i> -ratio	<i>P</i>	<i>df</i>	<i>F</i> -ratio	<i>P</i>	<i>df</i>	<i>F</i> -ratio	<i>P</i>	<i>df</i>	<i>F</i> -ratio	<i>P</i>
Between subjects												
Treatment	1	5.92	0.07	1	2.36	0.27	1	2.18	0.18	1	6.57	<i>0.04</i>
Block	6	4.54	0.08	6	6.18	0.15				6	1.42	0.34
Error	4			2			7			6		
Within subjects												
Month	2	1.87	0.22	3	53.8	<i>0.001</i>	3	6.62	<i>0.003</i>	1	7.14	<i>0.04</i>
Month×Treatment	2	0.15	0.87	3	0.45	0.73	3	0.67	0.58	1	4.47	0.08
Month×Block	12	0.92	0.57	18	5.91	<i>0.02</i>				6	1.31	0.38
Error	8			6			21			6		



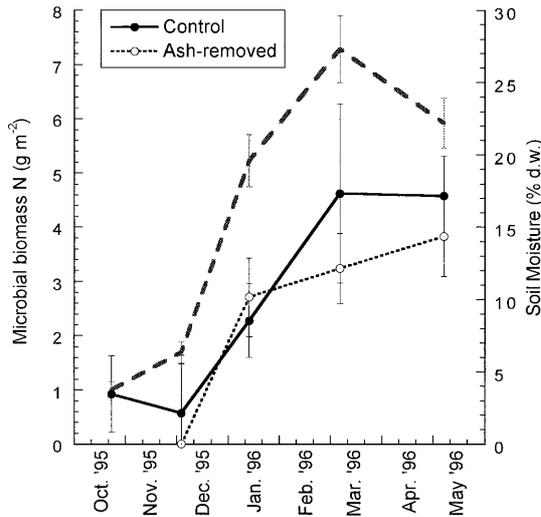
**Fig. 1** Above-ground biomass of each plant group at the end of the first growing season after fire ( $n=5-7$ , mean  $\pm$  SE). Statistically significant differences within each plant group at  $P < 0.05$  are indicated by an asterisk. The difference in *Pinus muricata* biomass reflects higher seedling density in the control plots that was not attributable to treatment (see Materials and methods)



**Fig. 2** The relationship between above-ground biomass and total below-ground N to 10 cm depth at the end of the first growing season after fire (biomass =  $1.68 \times \text{total N} - 137.74$ ;  $r = 0.89$ ,  $P < 0.001$ ,  $n = 12$ ). Total N does not include roots but does incorporate the ash layer in control plots



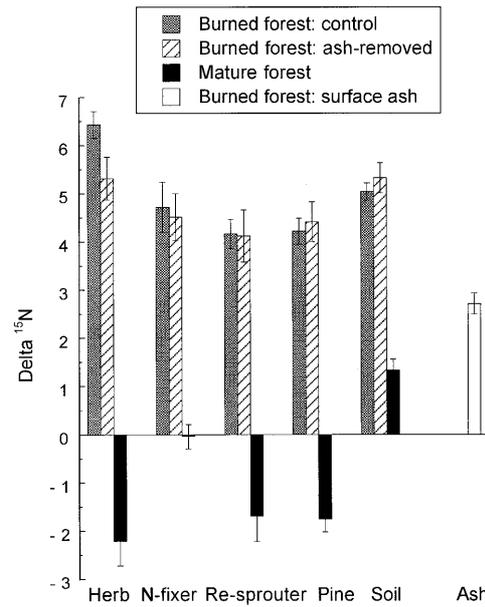
**Fig. 3** Soil inorganic N pools during the first two growing seasons after fire ( $n=7$ , mean $\pm$ SE). Nitrate ( $\text{NO}_3^-$ ) was below the detection limit ( $<0.5 \text{ mg N kg}^{-1}$ ) at the first and last sampling times



**Fig. 4** Microbial biomass nitrogen pools during the first growing season after fire ( $n=4-7$ , mean $\pm$ SE). Gravimetric soil moisture to 10 cm depth is indicated by the *thick dashed line* ( $n=7$ , mean $\pm$ SE)

mid-March (Table 3; Fig. 3). Since shoots of the re-sprouting species were first to emerge in early December, these results all point to a strong ash effect on soil N availability that resulted in enhanced above-ground plant N at the end of the growing season.

Microbial biomass N pools were stimulated by soil wet-up (Fig. 4), and increased significantly through the first growing season (Table 3), but were unaffected by the presence of ash. On the initial sampling date after the fire, mean microbial biomass N in deeper horizons (10–20 cm) was  $4.2 \text{ g N m}^{-2}$  ( $\text{SE}=1.4$ ) as compared to  $0.92 \text{ g N m}^{-2}$  in the upper surface 10 cm (Fig. 4). However, microbial biomass carbon to nitrogen ratios did not differ significantly between surface (mean=5.7,  $\text{SE}=1.3$ )



**Fig. 5**  $\delta^{15}\text{N}$  values in plant and soil N pools from recently burned and mature *P. muricata* forest stands (mean $\pm$ SE). Plant leaves from the same species were sampled in both stands (Herb *Stachys* sp., N-fixer *Ceanothus* sp., Re-sprouter *Rubus* sp., Pine *P. muricata*;  $n=5-7$ ). Soil  $\delta^{15}\text{N}$  values are to 10 cm depth below ground at the burned site ( $n=7$ ) and at the mature site ( $n=3$ ). The  $\delta^{15}\text{N}$  value for surface ash sampled immediately after the fire ( $n=4$ ) is also included

and deeper (mean=6.7,  $\text{SE}=1.0$ ) horizons at this time. These results indicate that heating effects of the fire severely diminished microbial biomass in the upper soil layer, reducing microbial N pools in all plots at the beginning of the growing season.

Fire resulted in a marked pulse of soil  $\text{NH}_4^+$  during the first growing season after fire (Fig. 3). Mean soil  $\text{NH}_4^+$  content in the surface 10 cm of a nearby unburned *P. muricata* forest stand was  $0.41 \text{ g N m}^{-2}$  ( $\text{SE}=0.05$ ) in late April 1998, two to four times less than values measured at the corresponding part of the first growing season after fire (Fig. 3). The soil  $\text{NH}_4^+$  pulse generated by fire was rapidly depleted due to both plant and microbial uptake (Table 2; Fig. 4). Soil  $\text{NO}_3^-$  pools significantly increased through the first growing season after fire (Table 3, Fig. 3) indicating microbial  $\text{NH}_4^+$  consumption by nitrifying bacteria. Soil  $\text{NH}_4^+$  pools in April 1997 (Fig. 3) were lower than in the mature forest at the same time of year (see above), suggesting that the fire-induced soil  $\text{NH}_4^+$  pulse had been dissipated by the end of the second growing season.

The presence of ash significantly elevated soil pH during the first growing season (Table 3). Ash increased mean soil pH from 4.6 to 5.2 pH units in December 1995 and from 5.1 to 5.4 pH units in May 1996.

Isotopic  $^{15}\text{N}$  natural abundance values contrasted sharply between recently burned and mature *P. muricata* stands (Fig. 5), suggesting strong effects of fire on N cycling below-ground. At the burned site, all plant and soil samples were highly enriched in  $^{15}\text{N}$ , suggesting that re-

establishing species access a common N source that shows minimal  $^{15}\text{N}$  depletion relative to the total soil N pool. These data also indicate that ecosystem N inputs via fixation of atmospheric N (which has a  $\delta^{15}\text{N}$  value of 0) were negligible in the first year after fire. By contrast, at the mature forest site, plant foliage from identical species was strongly  $^{15}\text{N}$  depleted in all species except the N-fixer (whose strong reliance on atmospheric N was indicated by  $\delta^{15}\text{N}$  values close to 0). The depletion of  $^{15}\text{N}$  in plant tissues at the unburned site contrasted markedly with the  $^{15}\text{N}$  enrichment observed in the soil organic horizon, indicating substantial fractionation of soil N prior to plant acquisition in mature forests.

## Discussion

Wildfires cause severe N losses through volatilisation and soil leaching (Grier 1975; DeBano and Conrad 1978; Raison 1979) and may be the primary mechanism contributing to N-limitation of primary production in fire-prone ecosystems (Vitousek and Howarth 1991). Our results demonstrate that ash residues deposited during wildfire can reduce ecosystem N losses by increasing soil N retention and enhancing plant N acquisition (Table 2). Plant N acquisition was enhanced because ash stimulated primary production by altering plant community structure in favor of resprouting species (Fig. 1). The capacity of resprouting species to rapidly produce new roots and shoots from surviving below-ground root stocks may explain their responsiveness to increased N availability. By contrast, N acquisition by species establishing from seed would be restricted by their relatively low initial biomass and by the time delay until the onset of appropriate germination conditions. Together, these results demonstrate that the deposition of ash residues during wildfire has important direct and indirect effects on ecosystem N retention and cycling after fire.

Fire commonly causes a large increase in soil  $\text{NH}_4^+$  (Christensen and Muller 1975; Raison 1979; Stock and Lewis 1986; Naveh 1990; Wienhold and Klemmedson 1992; Fenn et al. 1993), just as we observed, although the causes are often unclear. Since N accumulation in microbes and plant shoots at the end of the growing season (Table 2) greatly exceeded initial soil  $\text{NH}_4^+$  levels (Fig. 3), and N fixation was negligible (Fig. 5), substantial N must have been mineralised from below-ground organic sources in both ash and ash-free plots. An altered microenvironment due to the removal of above-ground vegetation and the darkened soil surface, and/or enhanced N mineralisation from soil organic matter that has been exposed to the heat of fires (Klopatek et al. 1990) could account for the enhanced soil  $\text{NH}_4^+$  pools after fire.

The surprising result from our experiments was the extent to which ash enhanced N availability and uptake by plants. Chemical analysis of the surface ash indicated a small direct addition of extractable  $\text{NH}_4^+$  to the soil pool from ash at the beginning of the growing season

(Table 2). Soil  $\text{NH}_4^+$  levels from December through to March tended to be higher ( $P=0.07$ ) in the presence of ash (Table 3, Fig. 3), despite greater plant N uptake, suggesting that ash also caused a prolonged N flux into the  $\text{NH}_4^+$  pool. Rates of  $\text{NH}_4^+$  production by soil microbes may have been stimulated by the increased pH following fire, which in other ecosystems raises the solubility of soil organic matter for decomposition (Raison 1979) and alters microbial community structure (Bååth et al. 1995). Total below-ground N to 10 cm depth was also significantly increased by the presence of ash (Table 2). The quantity of N contained in the ash accounted for about a third of this increase in total N (Table 2), with the remaining N presumably coming from improved retention of the insoluble soil organic N fraction in the upper soil horizon. Finally, the  $^{15}\text{N}$  data indicating similar  $\delta^{15}\text{N}$  values for plants and soil at the burned site and a markedly lower  $\delta^{15}\text{N}$  in surface ash (Fig. 5) suggest that ash enhanced plant N more by increasing turnover of soil organic N than by direct ash N input.

One potential artefact in our experiment is that we may have removed some surface soil dust from the treatment plots in the process of blowing off the ash. For removal of the uppermost surface soil to have influenced the results obtained with 10-cm-deep cores, N pools must decline rapidly with increasing soil depth. Surface soil  $\text{NH}_4^+$ , (but not total Kjeldahl-digestible soil N) is markedly increased by soil heating during fire (Stock and Lewis 1986; Klopatek et al. 1990). If, for example, we assume that the blower removed as much soil as ash (2.3 mm) and that this surface soil was tenfold more concentrated in  $\text{NH}_4^+\text{-N}$  than the rest of the soil in each sample core, the blowing treatment may have caused an unintended loss of  $0.4 \text{ g NH}_4^+\text{-N m}^{-2}$ . This effect along with the removal of the ash layer itself may explain the initial difference in  $\text{NH}_4^+\text{-N}$  levels between control and treatment plots immediately after the fire (Fig. 3). However, shoot N pools in the ash-removed plots at the end of the growing season were reduced by almost five times this amount (Table 2), indicating that this artefact has little potential impact on the main study conclusion that plant N acquisition was enhanced by ash.

The  $^{15}\text{N}$  natural abundance data indicate that fire greatly altered the pathways for N acquisition by plants in this ecosystem. The surface organic layer of mature coniferous forest floors tends to be depleted in  $^{15}\text{N}$  relative to deeper horizons because fractionation during mineralisation and plant uptake depletes the litter of  $^{15}\text{N}$  (Nadelhoffer and Fry 1988, 1994). Högberg (1997) proposed that the consumption of this  $^{15}\text{N}$ -depleted litter layer by fire exposes the mineral horizons below, resulting in relatively enriched  $^{15}\text{N}$  ratios in the re-establishing plant community. Nitrification, which discriminates strongly against  $^{15}\text{N}$ , can contribute to positive  $^{15}\text{N}$  foliage values in recently burned sites by enriching the substrate  $\text{NH}_4^+$  pool at the expense of leached nitrate losses (Högberg 1997). Our data demonstrating enriched plant  $^{15}\text{N}$  values (Fig. 5) and seasonally rising nitrate pools in the burned site (Fig. 3) support Högberg's hypotheses. Negligible

differences in  $\delta^{15}\text{N}$  values between shoot N and total Kjeldahl-digestible N below-ground are consistent with plant N acquisition from a fire-enhanced soil  $\text{NH}_4^+$  pool. The absence of a plant-soil difference in  $^{15}\text{N}$  suggests that the  $\text{NO}_3^-$  pools generated in the burned site (Fig. 3) are not acquired by plants in large quantities and may be lost via leaching or denitrification.

Plant  $\delta^{15}\text{N}$  values are influenced by rooting depth, mycorrhizal association and the form of inorganic N absorbed (Schulze et al. 1994). The similarity in  $\delta^{15}\text{N}$  values among plant species that re-established after fire (Fig. 5) suggests that these species used a common N pool, which showed minimal fractionation relative to the bulk soil N pool. By contrast, the data from an old *P. muricata* stand indicate that the same plant species (except the N-fixer) in a mature forest ecosystem acquire N that has been substantially fractionated during its mineralisation from the redeveloped litter/soil organic horizon (Fig. 5). The strong plant-soil difference in  $^{15}\text{N}$  and the similarity in  $\delta^{15}\text{N}$  values amongst species at the mature site suggest that plant uptake of  $\text{NO}_3^-$  may have contributed to the fractionation we observed. Recent research using laboratory incubations of forest soils in the absence of plants indicates that nitrification may be a much more dynamic and important component of coniferous forest N cycling than previously thought (Stark and Hart 1997). Our results provide field evidence for plant  $\text{NO}_3^-$  acquisition in mature forest communities and suggest that the fate of nitrate in conifer forest ecosystem N cycling is strongly altered by fire.

Ash production, nutrient content and physicochemical properties depend on the mass and composition of burned vegetation/litter as well as fire conditions (Raison 1979). The  $8.9 \text{ g N m}^{-2}$  input of N in ash that we observed is similar to values reported from a South African coastal shrub fynbos ecosystem ( $6.6 \text{ g N m}^{-2}$ ; Stock and Lewis 1986) and larger than estimates from Californian chaparral ( $2.1 \text{ g N m}^{-2}$ ; Christensen and Muller 1975) or a Washington conifer stand ( $2.3 \text{ g N m}^{-2}$ ; Grier 1975). Concentrations of total N in ash from the latter two studies were almost identical to our results, indicating that the higher ash total N input at our site was due to greater ash production. Surface ash is rapidly displaced by winds and rain after fire and accumulates in local hollows, on the leeward side of stumps/fallen trees, downslope in ravines and in nearby lakes (Wright 1976). Our results indicate that ash production and N input following wildfires can be substantially greater than previously reported and suggest that the redistribution of surface ash after fire may be a major factor contributing to heterogeneity in soil N availability and hence to vegetation patchiness in fire-prone ecosystems.

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