

# Factors Regulating Nitrogen Retention During the Early Stages of Recovery from Fire in Coastal Chaparral Ecosystems

Erin J. Hanan,<sup>1\*</sup> Carla M. D'Antonio,<sup>1</sup> Dar A. Roberts,<sup>2</sup>  
and Joshua P. Schimel<sup>1</sup>

<sup>1</sup>Department of Ecology, Evolution and Marine Biology, University of California Santa Barbara, Santa Barbara, California 93106, USA;  
<sup>2</sup>Department of Geography, University of California Santa Barbara, Santa Barbara, California 93106, USA

## ABSTRACT

Fire is a fundamental reorganizing force in chaparral and other Mediterranean-type ecosystems. Postfire nutrient redistribution and cycling are frequently invoked as drivers of ecosystem recovery. The extent to which N is transported from slopes to streams following fire is a function of the balance between the rate at which soil microbes retain and metabolize N into forms that readily dissolve or leach, and how rapidly recovering plants sequester this mobilized N. To better understand how fire impacts this balance, we sampled soil and plant N dynamics in 17 plots distributed across two burned, chaparral-dominated watersheds in Santa Barbara County, California. We measured a variety of ecosystem properties in both burned and unburned plots on a periodic basis for 2 years, including soil water content, pH, soil and plant carbon and

nitrogen, extractable inorganic nitrogen, dissolved organic nitrogen, and microbial biomass. In burned plots, nitrification was significantly enhanced relative to rates measured in unburned plots. Ephemeral herbs established quickly following the first postfire rain events. Aboveground plant biomass assimilated N commensurate with soil net mineralization, implying tight N cycling during the early stages of recovery. Microbial biomass N, on the other hand, remained low throughout the study. These findings highlight the importance of herbaceous species in conserving ecosystem nutrients as shrubs gradually recover.

**Key words:** disturbance; wildfire; xeric ecosystems; ash redistribution; nitrate leaching; mountainous landscapes; N-sinks.

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\*Corresponding author; e-mail: hanan@lifesci.ucsb.edu

## INTRODUCTION

Mediterranean-type ecosystems are structured by wildfire. In California chaparral, intense fires burn large areas (Keeley and Fotheringham 2001; Moritz 2003; Riggan and others 1988), stripping landscapes of vegetation, oxidizing nutrients (particularly N), and shrouding the terrain in nutrient-enriched ash and charred wood (Christensen 1973; Debano and Conrad 1978). The immediate effect of

fire is therefore to increase the bioavailability of all nutrients, but deplete N relative to P, K, and other more-stable elements. Fire promotes further short-term N loss by destroying soil aggregates and stimulating nitrate ( $\text{NO}_3^-$ ) production (Knicker 2007; Valeron and Meixner 2010), which can enhance leaching and erosion, particularly from slopes that have been denuded (DeBano and Conrad 1976). Although the rate and pattern of recovery in chaparral may depend on nutrient availability, it remains unclear how N-cycling processes, including mineralization and nitrification, balance against N-retention mechanisms, such as immobilization by recovering plants and microbes.

To understand the mechanisms driving N cycling and retention following fire, it is necessary to assess not only the immediate biogeochemical changes that set up the conditions for recovery, but also the subsequent processes that correspond with vegetation reestablishment and growth. Although chaparral does not exhibit seral stages as in "classical" forest succession (Vogl 1982), an early flush of ephemeral herbs and shortlived perennials still occurs. Species such as *Calystegia macrostegia* (coast morning glory), *Acmispon glaber* (deerweed), and various *Phacelia* spp. can establish rapidly and often dominate large portions of recovering hill slopes, although their composition and extent vary by location and among burn events (Davis and others 1989; Guo 2001; Keeley and others 2005; O'Leary 1988; Rundel and Parsons 1984). As has been well established in classical forest succession systems (for example, northeastern mixed forest, Henry and Swan 1974; boreal forest, Cleve and Viereck 1981; and Pacific northwestern coniferous forest, Franklin and Hemstrom 1981), the nature of early dominants in chaparral may play an important role in microbial dynamics, nutrient retention, and how rapidly the mature chaparral community recovers.

Ephemeral herbs that establish after fire can help retain and ultimately recycle N during the early stages of recovery when microbial and shrub biomass are both low (Rundel and Parsons 1984). This may be especially important in regions where N availability constrains plant growth, such as in stands dominated by *Adenostoma fasciculatum* or other non-N-fixing species (McMaster and others 1982), or in regions where atmospheric N deposition is low (Bytnerowicz and Fenn 1996; Schlesinger and others 1982). Ash-deposition and  $\text{NH}_4^+$  enrichment stimulate germination and N acquisition by rapidly growing ephemeral species (Christensen and Muller 1975; Grogan and others 2000), many of which appear to use N less efficiently than shrub species that persist in mature

ecosystems (ephemeral species have high N concentration in their foliage and litter; Swift 1991, as cited by Keeley and Keeley 2000). Thus, the role of vegetation as a nutrient sink may vary over space and time.

Microbial biomass can also play an important role in immobilizing N as ecosystems recover, and may therefore constrain N supply to vegetation. Fire can sometimes stimulate microbial population growth by providing a pulse of C and nutrients (Knicker 2007). However, microbial populations can subsequently decline once resources are depleted (Grasso and others 1996). This process may be prominent in chaparral, where crown fires consume most aboveground plant biomass and litter. Yet, in a chronosequence study, Fenn and others (1993) found no difference in microbial biomass C among chaparral stands ranging from 0 to 80 years. Thus, the effects of fire on microbial biomass might vary over space and time, and microbial biomass recovery has not been well characterized in chaparral.

After the first few postfire storm events, N export can rapidly return to baseline conditions (Verkaik and others 2013), which may reflect establishment and growth of ephemeral herbs, or recovery of microbial biomass. On the other hand, because N availability constrains plant growth in many chaparral ecosystems (Jenny and others 1950; Thanos and Rundel 1995), leaching and erosional losses that occur immediately after fire might in some cases slow plant recovery and associated N uptake, prompting a positive feedback on nutrient export. Under such circumstances, eventual reductions in stream N would more likely reflect diminishing rates of N mobilization. Although postfire N fluxes have been characterized in chaparral, the mechanisms driving these dynamics, such as the balance between mineralization and microbial immobilization versus plant uptake, are not well understood.

Although complete recovery in chaparral progresses over several decades, changes in vegetation and N redistribution are the most pronounced in the first few years (Li and others 2006; Schlesinger and Gill 1980). We therefore focused on N cycling during early recovery to better understand how soil processes regulate the relationships among plant growth, recovery of microbial biomass, and N retention in postfire chaparral systems. Specifically, we asked the following questions:

- (1) What factors influence net N mineralization and nitrification rates as chaparral ecosystems recover from fire?

- (2) What are the relative magnitudes of N sinks such as immobilization by microbial biomass, postfire herbs, and recovering shrubs?
- (3) How do N sinks compare to mobilized N?

To answer these questions, we measured soil and plant N dynamics in two fire-scarred watersheds in southern California. Large portions of these watersheds had burned in the November 2008 Tea Fire or the May 2009 Jesusita Fire.

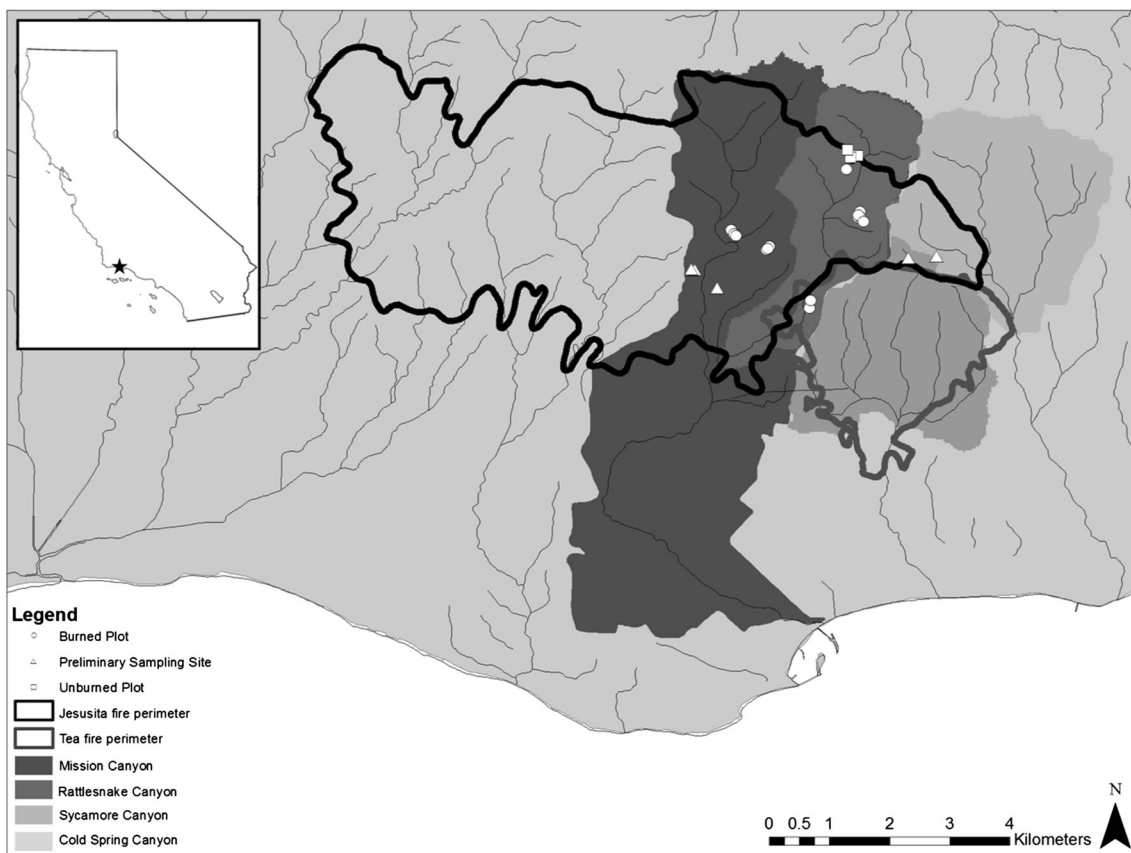
## METHODS

### Study Sites

Our study took place in chaparral watersheds along the southern facing slopes of the Santa Ynez Mountains in Santa Barbara County, California ( $34^{\circ}28'N$ ,  $-119^{\circ}40'E$ ; Figure 1). The rainy season typically begins in October or November, when rewetting dry soils triggers microbial respiration and mineralization pulses (Miller and others 2009). Cool wet winters support rapid plant growth; cha-

pparal communities develop canopies of closely spaced shrubs that range from 1.5 to 4 m tall (Davis and Mooney 1986). These shrubs have extensive fine woody stems and resinous waxy foliage. Thus, extensive conflagrations (that is, more than 10,000 hectares) are common, and in conjunction with smaller burns, produce fire return intervals averaging approximately 40–60 years in this region (Moritz 1997).

Two wildfires occurred in the study area in the last two decades: the Tea Fire in November 2008, and the Jesusita Fire in May 2009. Following the Jesusita Fire, study sites were established in the Mission Canyon and Rattlesnake Canyon watersheds approximately 6–10 km north of the Pacific Ocean (Figure 1). These watersheds are oriented approximately southward. Study site elevations ranged from 294 to 935 m (Table 1) and slopes ranged from 10 to 50%, although in some parts of these watersheds, slopes can reach 100%. Soils in the region are most commonly sandy loams, classified as Typic Dystrochrepts from the Maymen



**Figure 1.** Study site in Santa Barbara County, CA. Tea Fire, November 2008, 7.9 km<sup>2</sup>; Jesusita Fire, May 2009, 35.3 km<sup>2</sup>. 14 burned plots, 3 unburned plots, and 3 preliminary sampling regions located across the Mission Canyon and Rattlesnake Canyon watersheds.

**Table 1.** Distribution of Plots in Two Watersheds

Watershed	Fire	Plot	Bulk density	Elevation (m)	% Sand	% Silt	% Clay	Texture type	dNBR
Mission Canyon	Jesusita	JMC1	0.94 ± 0.03	374.7	52	29	19	Loam	601.9
		JMC2	0.93 ± 0.07	351.9	66	24	10	Sandy loam	642.0
		JMC3	0.90 ± 0.03	353.2	65	26	9	Sandy loam	733.3
		JMC4	1.10 ± 0.10	506.0	69	22	9	Sandy loam	767.2
		JMC5	1.06 ± 0.06	513.0	66	24	10	Sandy loam	883.7
		JMC6	1.03 ± 0.10	514.3	68	23	9	Sandy loam	840.3
Rattlesnake Canyon	Unburned	JR1	0.81 ± 0.04	653.3	47	29	24	Loam	673.1
		JR2	0.70 ± 0.06	694.5	65	23	12	Sandy loam	651.3
		JR3	0.83 ± 0.04	667.7	47	31	22	Loam	648.7
		JR4	0.69 ± 0.06	660.1	57	23	20	Sandy clay loam	852.2
		JR5	0.84 ± 0.06	664.3	39	35	26	Loam	445.6
		JR6	0.75 ± 0.18	855.4	75	18	7	Sandy loam	922.9
	Tea	UR1	0.74 ± 0.21	853.4	66	19	15	Sandy loam	-80.1
		UR2	1.10 ± 0.06	902.1	63	18	19	Sandy loam	13.2
		UR3	1.07 ± 0.05	935.0	76	16	8	Sandy loam	-28.2
		TR1	0.94 ± 0.08	277.8	65	24	11	Sandy loam	314.0
		TR2	1.06 ± 0.08	294.4	73	16	11	Sandy loam	206.7

Plots burned in either the Jesusita Fire, Tea Fire, or were unburned. Four sampling locations were established in each plot, and average bulk densities for the A horizon during the first sampling period are reported. Elevations (m), slope, aspect, soil texture, and dNBR are listed for each plot. Unburned dNBRs typically range from -100 to +99, low severity dNBRs range from +100 to +269, moderate severity dNBRs range from +270 to +659, and high severity dNBRs range from +660 to +1300.

series (NRCS 2015). Bedrock comprises sandstones and Quaternary alluvium and landslide breccia (DeBano and Conrad 1978).

Before the fires, three shrub species tended to dominate the study region: *Ceanothus megacarpus* (big pod ceanothus) mixed with *A. fasciculatum* (chamise) on the lower slopes, and *Arctostaphylos* spp. (manzanita) mixed with *A. fasciculatum* on the upper slopes. Other species such as *Malosma laurina* (laurel sumac), *Heteromeles arbutifolia* (toyon), and *Prunus ilicifolia* (holly-leaved cherry) also occurred in the area. Fires removed almost all vegetation and litter, leaving only small charred stumps in most sites. However, following rain, shrub resprouting, and seedling emergence were vigorous, with at least 60% of stumps resprouting (C.M. D'Antonio unpublished). Postfire herbs also established rapidly after rain. In sites that burned in the Jesusita Fire, the fast-growing vine *C. macrostegia* (coast morning glory) formed a thick layer, while sites that burned in the Tea Fire were rapidly colonized by the N-fixing suffrutescent *A. glaber* (deerweed).

## Remote Sensing

To quantify fire severity at our study sites, we used hyperspectral remote-sensing imagery collected by the Airborne Visible/Infrared Imaging Spectrometer (AVIRIS; Green and others 1998). Fire severity refers to the degree to which an ecosystem is trans-

formed by fire, and includes charring, consumption of plant biomass, and mortality (Keeley 2009). The Normalized Burn Ratio (NBR) and differenced NBR (dNBR) indices use shortwave infrared (SWIR; 0.9–1.7 μm) reflectances to characterize fire severity across the landscape. Using AVIRIS, SWIR bands effectively separate non-photosynthetic wood from soil and charred wood following fire (Miller and Thode 2007; Van Wagendonk and others 2004).

AVIRIS datasets were obtained for the Santa Barbara area for flights occurring before and after the fires. The before-fire flight was on August 6th 2004. Although the 2004 imagery was taken almost 5 years before the fire, the vegetation in the region had not changed much in the intervening time since there had not been a fire in the region since 1964. Because chaparral reaches a more or less steady state of biomass and composition within 20 years (Schlesinger and Gill 1980), we consider this scene to be a reasonable representation of prefire conditions. The postfire dataset was obtained from a flight on August 26th 2009 (9 months after the Tea Fire and 3 months after the Jesusita Fire). These datasets were atmospherically corrected, converted to reflectance and georectified. The August 26th 2004 dataset was originally acquired at 16 m resolution, then resampled to 12 m resolution using nearest neighbor resampling (Jia and others 1999) to match the 12-m resolution of the August 6th 2009 dataset. Normalized Burn

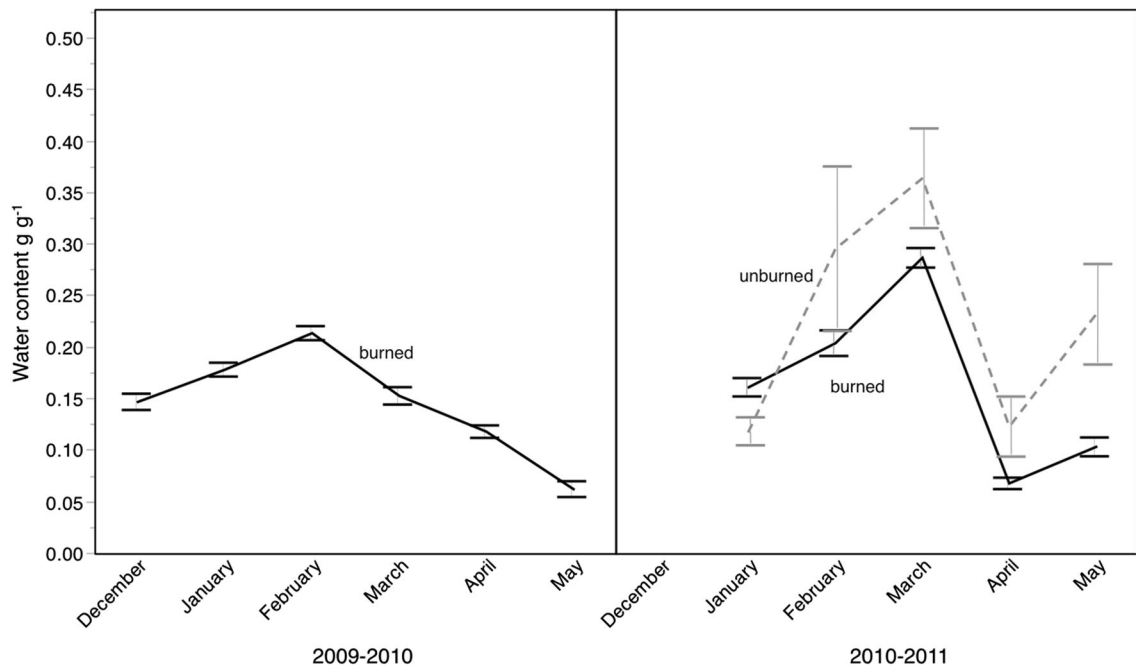


Figure 2. Monthly gravimetric water content in burned and unburned chaparral during the 2009–2010 and 2010–2011 growing seasons.

Table 2. Distribution of Preliminary Sampling Sites

Watershed	Fire	Location	Bulk density	Elevation (m)	% Sand	% Silt	% Clay	Texture type	dNBR
Mission Canyon	Jesusita	1	1.17 ± 0.10	252.7	44	30	26	Loam	800.2
		2	1.06 ± 0.13	268.6	68	20	12	Sandy loam	410.9
		3	0.99 ± 0.19	279.1	70	18	12	Sandy loam	540.8

Four samples were collected at 5 m intervals from each site, and average bulk densities for the A horizon during the first sampling period are reported. Elevations (m), slope, aspect, soil texture, and dNBR are listed for each plot.

Ratios (NBRs) were calculated for AVIRIS scenes using the following formula:

$$NBR = 1000([\rho_{788} - \rho_{2370}]/[\rho_{788} + \rho_{2370}]) \quad (1)$$

where  $\rho$  represents reflectance at a given wavelength (that is, 788 and 2370 nm). Individual flight lines were subsequently masked, stitched, and resampled as necessary to assure that images for each year covered identical spatial extents. NBRs are scaled by 1000 to provide more-easily interpretable integer values. Differenced NBRs (dNBRs) were calculated using formula 2:

$$dNBR = NBR_{\text{prefire}} - NBR_{\text{post-fire}} \quad (2)$$

using prefire NBR obtained from the August 6th 2004 scene, and postfire NBR obtained from the August 26th 2009 scene. Field sampling points

were imported over the dNBR layers and dNBR values were extracted for each point.

### Field Sampling

To evaluate the relationship between postfire N cycling and immobilization, study plots were established in November 2009 and monitored on an approximate monthly basis between December 2009 and May 2011. Fifteen, 15 m by 15 m burned plots were delineated at random points in eight generally large (>500 m<sup>2</sup>) and irregularly shaped polygons of known prefire vegetation composition located in the Jesusita and Tea Fire scars. Polygons were established prior to burning for a remote-sensing vegetation map (Roth and others 2012). Plots were organized into the Mission Canyon and Rattlesnake Canyon watersheds. Mission Canyon

and Upper Rattlesnake Canyon burned in the Jesusita Fire, whereas Lower Rattlesnake Canyon burned in the Tea Fire (Figure 1). Elevations ranged from 277 to 935 m.

In December 2010, three plots that had not burned for 46 years were established in the Rattlesnake Canyon watershed to compare N fluxes in mature chaparral to those in burned sites (Figure 1; Table 1). It was impossible to establish additional unburned plots in the Mission Canyon watersheds because the only remaining unburned vegetation was within dense riparian habitat or along extremely steep terrain that was inaccessible (Figure 2). On October 12, 2009, prior to establishing our study plots and prior to any rainfall, four soil cores, each spaced 5 m apart, were collected from each of three sampling locations within the Mission Canyon watershed (in close proximity to where the 15 × 15 m plots were later established; Figure 1; Table 2). These are referred to as preliminary samples. All preliminary sampling sites had burned in the Jesusita Fire. These three sites were resampled in the same location on October 22, 2009 (after the first storm event of the season), to capture the effects of initial wetting on post-burn N pools. All soil samples were brought back to the laboratory for analysis. Thereafter, all soil sampling occurred within the 15 × 15 m plots.

### Soil Physical and Chemical Properties

In each 15 × 15 m plot, four in situ field-incubation cores were established using a version of the DiStefano and Gholz (1986) procedure for measuring net N transformations in situ. To establish incubation cores, 5-cm diameter by 15 cm deep polyvinyl chloride tubes were driven into the ground and removed with intact soil. A small amount of soil from the bottom of each core was removed and replaced with a nylon bag containing approximately 15 g of mixed bed ion exchange resin (J.T. Baker, Center Valley, PA). Resin bags were fitted with coated wire rings that spread resin evenly and snugly across the bottom of each core. Cores were returned to the hole from which they were extracted, and adjacent cores were collected to establish preincubation conditions. Each autumn through spring month over a two-year period, incubation cores were extracted and analyzed, and new cores were deployed immediately adjacent to where the previous cores were extracted. This technique is superior to many in situ net N-mineralization assays because it allows moisture in the cores to fluctuate, and the products of mineralization and nitrification can leach from the cores, but

will be captured by the ion exchange resins (Binkley and Hart 1989). However, water content in these cores may still be greater than in surrounding areas (Hart and Firestone 1989). Nevertheless, net mineralization measurements provide a useful comparative index of overall inorganic N availability (Schimel and Bennett 2004). In each plot, two cores were maintained adjacent to live resprouting shrubs, and two in initially open areas.

All soil samples were homogenized and run through a 4-mm sieve. Bulk densities were determined for subsamples as oven-dry mass equivalent of the less than 4-mm fraction divided by core volume. Water-holding capacity and gravimetric water content were determined by weighing 10-g wet subsamples, then saturating them with water. Subsamples were reweighed and then dried at 65°C for 72 h. Soil pH was measured using 10-g wet subsamples slurried (1:1 by mass) with deionized water (Jones 2001). Total carbon (TC) and nitrogen (TN) concentrations were determined using a Carlo Erba/Fisons, NA 1500 Series 2 elemental analyzer (Beverly, MA). Soil particle size (texture) was analyzed on samples composited from each of the four sampling locations within each plot, using the hydrometer method (Sheldrick and Wang 1993). Texture analyses were performed at the Division of Agriculture and Natural Resources Analytical Laboratory, University of California Cooperative Extension (Davis, CA).

### Inorganic N Pools

Extractable  $\text{NH}_4^+$  and  $\text{NO}_3^-$  were determined for all soil and resin samples by either extracting 10 g soil (wet weight), or all resin contained in each disk in 0.5 M  $\text{K}_2\text{SO}_4$  (40 mL) for 4 h then vacuum filtering through a glass fiber filter (Pall Gelmann Type A/E 1.0  $\mu\text{m}$ ). Extracts were frozen until analysis. Inorganic N concentrations were analyzed using a Lachat autoanalyzer (2003).  $\text{NH}_4^+$  was analyzed by increasing the pH of the flow stream, converting  $\text{NH}_4^+$  to  $\text{NH}_3$ , which diffuses across a Teflon membrane into an acidic medium that contains a pH indicator.  $\text{NH}_4^+$  in the sample is calculated from the pH change in the indicator solution.  $\text{NO}_3^-$  was reduced by Cd followed by Griess-Ilosvay reaction, and analyzed colorimetrically. Net N mineralization was considered to be the amount of inorganic N ( $\text{NH}_4^+$  and  $\text{NO}_3^-$ ) that accumulated in the soil core plus the amount that accumulated on the resin minus the amount of inorganic N measured in the preincubation core. Net nitrification rates were determined analogously, using only  $\text{NO}_3^-$  concentrations in the calculation. All results were

normalized to  $\mu\text{g g}^{-1}$  dry weight of soil in the core, and were scaled to  $\text{g m}^{-2}$  using average bulk density for each initial and incubated core pair in order to compare soil inorganic N dynamics with plant uptake rates.

#### *Microbial Biomass C and N*

Microbial biomass was determined by the chloroform slurry-extraction method (Fierer and Schimel 2002). The efficiencies of biomass extraction using this method are not significantly different from traditional chloroform vapor extraction methods (Fierer 2003). Ten g subsamples were extracted with 40 mL of 0.5 M  $\text{K}_2\text{SO}_4$  and 0.5 mL of  $\text{CHCl}_3$ , and filtered as above. Non-purgeable organic carbon (NPOC) and total nitrogen (TN) contents of  $\text{CHCl}_3$ -fumigated and -unfumigated extracts were measured using a Shimadzu Corporation, Series V Model CSN analyzer. Extractable microbial biomass C and N were calculated as the difference in organic C and N between the  $\text{CHCl}_3$ -treated and the corresponding untreated subsample. Because  $\text{CHCl}_3$  releases only a fraction of total microbial biomass C and N, conversion factors of 0.45 for C (Beck and others 1997) and 0.54 for N (Brookes and others 1985) were used to estimate total microbial biomass C and N. Extractable organic carbon (EOC) was calculated as the NPOC of non- $\text{CHCl}_3$ -treated samples. Extractable organic nitrogen (EON) was estimated as extracted TN minus inorganic N. Results were normalized to  $\mu\text{g g}^{-1}$  dry weight.

#### Vegetation Monitoring

We evaluated the species composition, structure, and N content of recovering vegetation by sampling at peak biomass during the 2009–2010 and 2010–2011 growing seasons. Measurements were taken in June, during the flowering of ephemeral herbaceous species, but prior to their senescence. To determine total biomass, percent moisture, and N and C content for both live and dead vegetation, we harvested twelve  $1\text{-m}^2$  subplots aboveground within each  $15 \times 15$  m plot using a stratified random point grid cut at the ground surface. Subplots were located at random distances along three evenly spaced transects established for percent cover measurements. Subplots harvested during the first growing season were marked, and excluded from harvest during the second year. Weights were determined for all shrub and herbaceous species within each subplot and subsamples of harvested biomass were brought to the laboratory for dry weight corrections and nutrient analyses. Plant TC and TN concentrations were determined using a

Carlo Erba/Fisons, NA 1500 Series 2 elemental analyzer, and results were normalized to  $\text{g m}^{-2}$  based on each species average cover value.

To evaluate plant N uptake in aboveground biomass in burned plots, changes in plant biomass were calculated for each growing season. Species were categorized by growth form (herbaceous or shrub). All aboveground biomass was considered new aboveground growth for both herbs and shrubs during the 2009–2010 growing season. New biomass in 2010–2011 was calculated as total plant biomass minus shrub biomass from the previous season. In year one, all litter was clearly produced in that year, as the plots were initially bare. At the start of the second growing season, no litter was obvious on the ground, suggesting all litter had decomposed or blown away. Given the timing of rainfall and plant senescence, it is unlikely that very much N was lost from that litter. Therefore, litter was assumed to be senesced material from the growing season during which it was collected, and was factored into total biomass calculations. To determine an index of N availability, soil net mineralized N was converted to  $\text{g m}^{-2}$  growing season<sup>-1</sup>. Values were then compared with aboveground plant uptake, estimated as biomass of species  $\times$  times N concentration of that tissue, to evaluate the potential for N limitation to plant growth in each sampling area following fire.

#### Statistical Analysis

To evaluate the extent to which soil physical properties varied between watersheds and between burned and unburned plots, we used 2-way analysis of variance. Watershed and burn status were both considered fixed effects, and response variables were (1) percent sand, (2) percent silt, (3) percent clay, and (4) bulk density. We also used linear regressions to evaluate whether the above response variables varied with elevation.

To evaluate postfire N-cycling dynamics, we used repeated-measures analysis of variance. The beginning of the incubation period was considered a categorical within-subject variable, while watershed sampled was considered a between-subjects factor. Because we did not sample during summer months, and Tea Fire plots were added during the 2nd year of analysis, we analyzed the 2009–2010 and the 2010–2011 sampling years separately. For the 2010–2011 sampling year, we also added fire event (that is, Jesusita vs. Tea) as an additional between-subjects factor. Then to compare N dynamics with patterns observed in mature chaparral, we restricted our analysis to upper Rat-

tlesnake Canyon, where we had six plots that burned in the Jesusita Fire coupled with three adjacent unburned plots. Although this reduced the sample size for burned sites, it increased the proximity of burned and unburned as a whole. As above, we used two-way repeated-measures analysis of variance to evaluate whether N dynamics varied between burned and mature plots. Again, month was considered a within-subject variable, whereas burn status was considered a between-subjects factor. For both sets of analyses, plots were considered replicates within each factor combination. Cores were treated as subsamples, and values were averaged within for each replicate plot. Response variables were (1) soil water content, (2) soil pH, (3)  $\text{NH}_4^+$  pools, (4)  $\text{NO}_3^-$  pools, (5) microbial biomass C content, (6) microbial biomass N content, (7) extractable organic nitrogen (EON), (8) net N mineralization, and (9) nitrification. A Greenhouse-Geisser correctional adjustment, which adjusts the degrees of freedom for the F statistic, was applied for all response variables in the 2009–2010 growing season. In the 2010–2011 growing season, a Greenhouse-Geisser correction was applied for all response variables except soil moisture, microbial biomass C, microbial biomass N, and extractable organic N, which did not violate the assumption of sphericity. For all analyses,  $P < 0.1$  was considered statistically significant since it was indicative of a strong trend, and with small sampling sizes, using a  $P < 0.05$  would create an excessive risk of Type-II error (Hurlbert and Lombardi 2009).

## RESULTS

### Remote Sensing

Fire severities (as measured by dNBR) were moderate to high across regions that burned in the Jesusita and Tea fires; they were highest in the Mission Canyon and Rattlesnake Canyon plots that burned in the Jesusita Fire (Table 1). dNBRs ranging from  $-100$  to  $+99$  are considered to be unburned,  $+100$  to  $+269$  are considered low severity,  $+270$  to  $+659$  are considered moderate severity, and  $+660$  to  $+1300$  are considered high severity (Key and Benson 2004). Our dNBR values ranged from  $410.9$  to  $922.9$  at sites that burned in the Jesusita Fire,  $206.7$  to  $314.0$  at sites that burned in the Tea Fire, and  $-80.1$  to  $13.2$  at unburned sites (Tables 1, 2). Tea Fire values likely underestimate fire severity because postfire NBRs were derived from the August 2009 scene, 9 months after the fire occurred, and included some postfire regrowth by annuals followed by senescence in August 2009.

### Soil Characteristics

To explore the extent to which observations in burned areas might have resulted from site differences (in addition to the effects of fire), we evaluated how soil texture and bulk density varied among plots. Soil texture was similar among plots, and ranged from loam to sandy-loam (Tables 1, 2). Percent sand, silt, and clay did not vary with elevation ( $R^2 < 0.03$  in all cases), and there were no consistent trends between watersheds ( $P > 0.25$  for all three parameters). Bulk densities ranged from  $0.7$  to  $1.1 \text{ Mg m}^{-3}$ , and decreased slightly with elevation ( $y = -0.0003x + 1.0761$ ;  $R^2 = 0.17$ ). Unlike texture, bulk density was significantly higher in Mission Canyon than in Rattlesnake Canyon ( $P = 0.01$ ); however, it did not vary between burned and unburned sites (at least in soils collected from the A-horizon; Table 1). Soil moisture varied seasonally in all plots (Table 3; Figure 2; Online Appendix 1–6). During the first year of study, soil moisture levels increased between December 2009 and February 2010 and then decreased through the following May. In the second year, soil moisture peaked in March 2011, and then late-season rain produced a second moisture pulse in May 2011. Moisture fluctuations in unburned chaparral were similar to those in burned chaparral, but unburned plots were significantly wetter ( $p = 0.10$ ; Figure 2, Online Appendix 6).

Soil pH was around 6.5 in burned sites during the first year of study (Figure 3). After an initial increase in December and January, pH decreased significantly over time ( $P < 0.01$ ; Table 3; Figure 3; Online Appendix 1). There was no significant interaction between time and watershed for pH during the first growing season, indicating that the pattern of decline was similar between watersheds (Online Appendix 1). By the second year of study, pH matched the values in unburned sites (around 5.45).

### N and C Dynamics

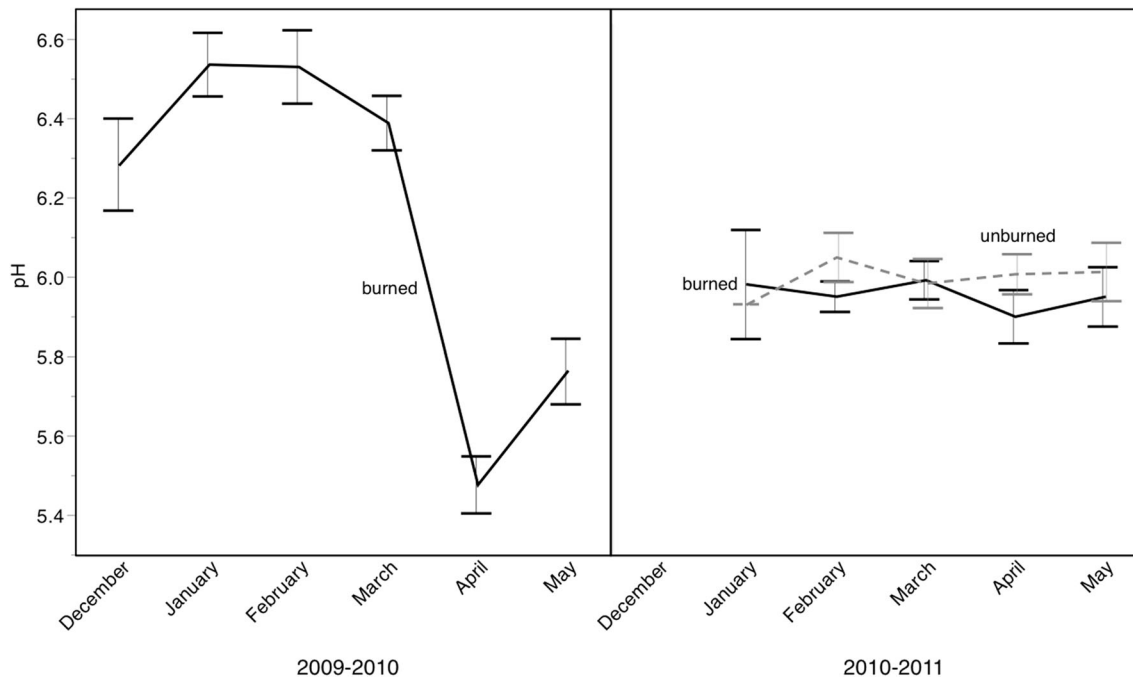
In the first year of study, soil samples from burned areas were enriched in  $\text{NH}_4^+$  relative to those collected later (Figure 4). Over the course of the study, inorganic N concentrations were higher in Rattlesnake Canyon plots that burned in the Jesusita Fire, than in Mission Canyon plots or in Rattlesnake Canyon plots that burned in the Tea Fire (Table 4; Figure 5; Online Appendix 1–6), corresponding with higher total C and N (Table 4). During both years, increases in soil moisture coincided with  $\text{NH}_4^+$  production in both burned and



**Table 3.** Mean Parameter Values  $\pm$  1 SE for Soils Collected Prior to Plot Setup

	Pre-rain	Post-rain
Soil moisture %	3.2 $\pm$ 0.5	13.9 $\pm$ 1.0
pH	6.5 $\pm$ 0.2	6.7 $\pm$ 0.2
Total C (mg g <sup>-1</sup> )	56.7 $\pm$ 10.1	
Total N (mg g <sup>-1</sup> )	3.3 $\pm$ 0.5	
Biomass C ( $\mu$ g g <sup>-1</sup> )	1269.5 $\pm$ 346.1	648.1 $\pm$ 285.4
Biomass N ( $\mu$ g g <sup>-1</sup> )	82.5 $\pm$ 18.5	66.5 $\pm$ 33.7
Extractable organic C ( $\mu$ g g <sup>-1</sup> )	1112.9 $\pm$ 201.1	122.2 $\pm$ 24.8
Extractable organic N ( $\mu$ g g <sup>-1</sup> )	69.7 $\pm$ 15.2	1.3 $\pm$ 0.9
NH <sub>4</sub> <sup>+</sup> -N ( $\mu$ g g <sup>-1</sup> )	41.5 $\pm$ 4.9	26.1 $\pm$ 5.0
NO <sub>3</sub> <sup>-</sup> -N ( $\mu$ g g <sup>-1</sup> )	9.9 $\pm$ 5.5	15.9 $\pm$ 3.1

Pre-rain samples were collected on October 12, 2009 and post-rain samples were collected on October 22, 2009 (mean values are for all three sampling sites, each site containing 4 samples).

**Figure 3.** Monthly pH in burned and unburned chaparral during the 2009–2010 and 2010–2011 growing seasons.

unburned sites. As a result, soil NH<sub>4</sub><sup>+</sup> concentrations and net N mineralization varied significantly over time ( $P < 0.01$ ; Table 5; Online Appendix 1, 3). However, significant interactions between time and watershed indicate that net N-mineralization dynamics also varied spatially, but only during the first few months of the growing season ( $P < 0.01$ ; Online Appendix 1). Also, both NH<sub>4</sub><sup>+</sup> and net N mineralization were significantly higher in soils collected from plots that burned in the Jesusita Fire than in those collected from adjacent unburned areas ( $P < 0.01$ ; Table 4; Online Appendix 6).

Nitrate concentrations did not vary among burned watersheds (Online Appendix 3, 4), but they were significantly higher in plots that burned in the Jesusita Fire than they were in plots that burned in the Tea Fire (Online Appendix 3, 4). Soil NO<sub>3</sub><sup>-</sup> concentrations and nitrification were both significantly higher in burned than in unburned plots ( $P < 0.01$ ; Table 4; Figures 4, 5; Online Appendix 6). Enhanced NO<sub>3</sub><sup>-</sup> concentrations in burned sites corresponded with elevated pH and NH<sub>4</sub><sup>+</sup> concentration during the first year of study (Table 4; Figures 3, 4). However, both NH<sub>4</sub><sup>+</sup> con-

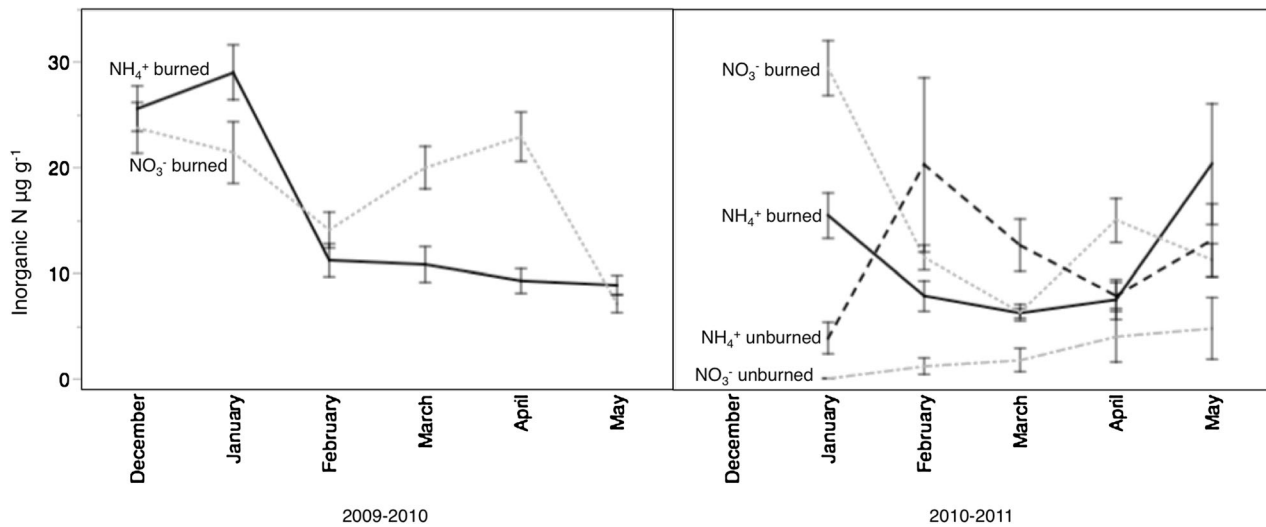


Figure 4. Inorganic N pools in burned and unburned chaparral during the 2009–2010 and 2010–2011 growing seasons.

centrations and pH decreased in burned soils during the second year of study, while  $\text{NO}_3^-$  remained high (Tables 4, 5; Figures 3, 4).

During both years of study, extractable organic C (EOC) and extractable organic N (EON) decreased significantly over time in both burned and unburned sites ( $P > 0.01$  for both parameters in year 1;  $P = 0.05$  and  $0.00$ , respectively, in year 2; Online Appendix 1 and 3). Significant interactions between time and watershed during the first year of study indicate that EOC and EON dynamics also varied spatially ( $P = 0.01$  and  $0.00$ , respectively; Online Appendix 1). Similar to inorganic N, EOC and EON were significantly higher in Rattlesnake Canyon plots that burned in the Jesusita Fire, than in Mission Canyon plots during the first year of study ( $P > 0.01$  and  $0.01$ , respectively; Online Appendix 2), whereas in year 2 only EOC was higher ( $P = 0.01$ ; Online Appendix 4). Extractable organic C was also higher in Rattlesnake Canyon sites that burned in the Jesusita Fire than in those that burned in the Tea Fire ( $P = 0.10$ ; Online Appendix 4). When comparing EOC in burned and unburned sites in Rattlesnake Canyon, there was a significant interaction between burn status and time ( $P = 0.02$ ; Online Appendix 5). Extractable organic C was higher initially in burned plots and decreased over time, while it started low in unburned areas but increased more during storm events.

Changes in microbial biomass between sampling dates were higher in burned plots than in unburned plots (Tables 3, 4; Figure 6). In burned areas, microbial C and N were high immediately after fire (even prior to the onset of autumn rain; Table 3).

However, microbial biomass then decreased significantly over the first postfire growing season to levels below those in unburned areas ( $P < 0.01$  and  $0.05$ , respectively; Figure 6; Online Appendix 1), and did not vary over time during the second year of study (Table 5; Online Appendix 3).

### Nutrient Immobilization by Recovering Vegetation

Plant N sequestration was similar between Upper Rattlesnake Canyon and Mission Canyon (Table 5). Plant N was more than 2 times higher in Lower Rattlesnake Canyon than in any other area (during both years of sampling), which burned in the Tea Fire and was therefore one growing season ahead in its recovery. Tea Fire sites also contained a larger proportion of N fixing species (that is, *C. megacarpus* and *A. glaber*; Table 5). During the first year of study, more than half of plant biomass N across all plots was contained in herbaceous species. N contained in aboveground plant biomass increased slightly in all sites between the first and second growing seasons, although increases were small relative to biomass C. Plant N sequestration (estimated as aboveground plant N uptake) over each growing season exceeded net N mineralization-rates (Table 5).

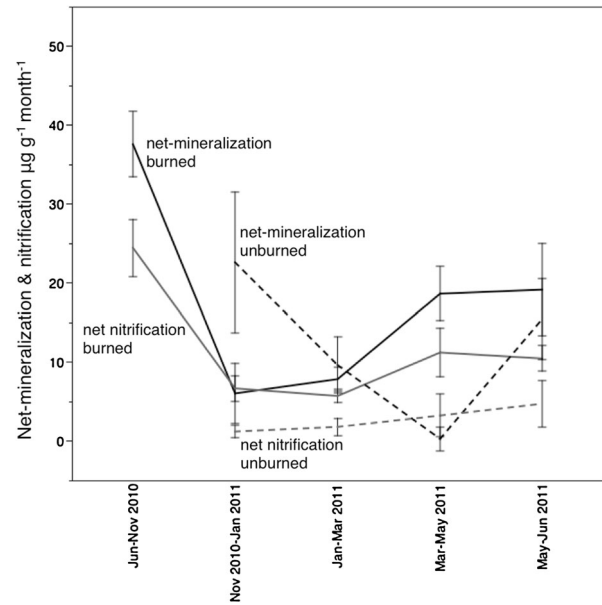
### DISCUSSION

Fires transform chaparral ecosystems, leaving behind a mosaic of dead and scorched vegetation, charred wood, hydrophobic oils and resins, and nutrient-rich ash. These residues interact with autumn and winter

**Table 4.** Mean Parameter Values  $\pm$  1 SE for Each Sampling Region During the 2009–2010 and 2010–2011 Growing Seasons

	Mission Canyon		Rattlesnake Canyon		Tea Fire	
	Jesusita Fire		Jesusita Fire		Unburned	
	2009–2010	2010–2011	2009–2010	2010–2011	2010–2011	2010–2011
Total C ( $\text{mg g}^{-1}$ )	21.6 $\pm$ 0.5	16.2 $\pm$ 1.1	52.8 $\pm$ 2.2	39.7 $\pm$ 6.3	23.8 $\pm$ 4.9	24.7 $\pm$ 2.1
Total N ( $\text{mg g}^{-1}$ )	1.3 $\pm$ 0.0	0.9 $\pm$ 0.1	3.5 $\pm$ 0.1	2.3 $\pm$ 0.4	0.9 $\pm$ 0.2	1.5 $\pm$ 0.1
Biomass C ( $\mu\text{g g}^{-1}$ )	45.6 $\pm$ 18.1 <sup>1</sup>	72.0 $\pm$ 8.9 <sup>a</sup>	329.1 $\pm$ 50.5 <sup>2</sup>	229.9 $\pm$ 38.2 <sup>bc</sup>	377.4 $\pm$ 54.0 <sup>c</sup>	141.1 $\pm$ 20.0 <sup>ab</sup>
Biomass N ( $\mu\text{g g}^{-1}$ )	4.9 $\pm$ 1.7 <sup>1</sup>	5.2 $\pm$ 1.2 <sup>a</sup>	21.7 $\pm$ 4.7 <sup>2</sup>	14.6 $\pm$ 3.0 <sup>ab</sup>	28.8 $\pm$ 5.3 <sup>b</sup>	7.6 $\pm$ 1.7 <sup>a</sup>
Extractable organic C ( $\mu\text{g g}^{-1}$ )	53.7 $\pm$ 5.4 <sup>1</sup>	21.1 $\pm$ 12.0 <sup>a</sup>	118.8 $\pm$ 11.2 <sup>2</sup>	29.0 $\pm$ 5.7 <sup>b</sup>	20.1 $\pm$ 3.9 <sup>b</sup>	8.4 $\pm$ 1.7 <sup>c</sup>
Extractable organic N ( $\mu\text{g g}^{-1}$ )	5.3 $\pm$ 1.0 <sup>1</sup>	1.3 $\pm$ 0.5 <sup>ab</sup>	17.8 $\pm$ 3.2 <sup>2</sup>	1.8 $\pm$ 0.8 <sup>a</sup>	5.5 $\pm$ 1.9 <sup>b</sup>	0.9 $\pm$ 0.3 <sup>ab</sup>
NH <sub>4</sub> <sup>+</sup> -N ( $\mu\text{g g}^{-1}$ )	15.9 $\pm$ 1.1 <sup>1</sup>	10.8 $\pm$ 1.6 <sup>a</sup>	14.7 $\pm$ 1.5 <sup>1</sup>	8.9 $\pm$ 1.2 <sup>a</sup>	13.6 $\pm$ 2.5 <sup>b</sup>	9.2 $\pm$ 2.9 <sup>ab</sup>
NO <sub>3</sub> <sup>-</sup> -N ( $\mu\text{g g}^{-1}$ )	10.6 $\pm$ 0.8 <sup>1</sup>	12.1 $\pm$ 1.2 <sup>a</sup>	25.7 $\pm$ 1.6 <sup>2</sup>	21.2 $\pm$ 2.1 <sup>a</sup>	2.9 $\pm$ 1.0 <sup>b</sup>	9.9 $\pm$ 1.5 <sup>b</sup>
Net-mineralization ( $\mu\text{g g}^{-1} \text{ month}^{-1}$ )		7.7 $\pm$ 1.7 <sup>a</sup>		13.7 $\pm$ 2.6 <sup>a</sup>	10.8 $\pm$ 2.9 <sup>a</sup>	8.6 $\pm$ 3.1 <sup>a</sup>
Net-nitrification ( $\mu\text{g g}^{-1} \text{ month}^{-1}$ )		7.0 $\pm$ 1.5 <sup>a</sup>		16.4 $\pm$ 2.3 <sup>b</sup>	2.7 $\pm$ 1.0 <sup>a</sup>	9.0 $\pm$ 1.5 <sup>ab</sup>

Mean values are for all plots in each region. Total C and total N were measured at the beginning and end of the study. All other pools were measured monthly and are averaged over the growing season for each year. Significant differences among sampling regions for each year are indicated with superscripts—2009–2010 differences are indicated with integers, and 2010–2011 differences are indicated with letters.



**Figure 5.** Monthly net mineralization and nitrification in burned and unburned chaparral during the 2010–2011 growing season.

rain to determine the fate of mineral N as ecosystems recover (Certini 2005; Debanco and Conrad 1978; Dunn and others 1979; Grogan and others 2000; Knicker 2007; Neary and others 1999). An inherent challenge associated with studying wildfires is that these systems are complex, and severe landscape fires are by nature unreplicable. Because each plot was associated with only one of the two fires, or had not burned, the effects of fire were potentially confounded with environmental variability among plots, with differences in time since fire, and with differences in fire behavior. While these analyses do not allow us to completely rule out the confounding effects of environmental variability on N dynamics, we were able to evaluate recovery trajectories over time, and infer patterns that were associated with the fires (Quinn and Keough 2002).

We found that net nitrification was enhanced for at least 2 years following fire, while aboveground plant regrowth sequestered large amounts of N relative to annual net N mineralized. Belowground N uptake can even further increase this sink, implying surprisingly tight N cycling during the early stages of recovery. This contradicts the conventional view that nutrients are in excess immediately following disturbance (Vitousek and Melillo 1979). Microbial biomass N on the other hand remained low in the first few years of recovery. Hence, plant regrowth plays an important role in retaining N after fire in chaparral, whereas microbial biomass does not.

**Table 5.** Net Mineralization and Aboveground Plant Biomass C and N Accumulated Over Each Growing Season

	Mission Canyon						Rattlesnake Canyon							
	Jesusita Fire			Jesusita Fire			Jesusita Fire			Tea Fire				
	C	N		C	N		C	N		C	N			
	2009–2010	2010–2011	2009–2010	2010–2011	2009–2010	2010–2011	2009–2010	2010–2011	2009–2010	2010–2011	2009–2010	2010–2011	2009–2010	2010–2011
Net-mineralization	–	–	1.5 ± 0.1	1.2 ± 0.1	–	–	1.5 ± 0.1	1.0 ± 0.1	–	–	–	–	–	1.1 ± 0.4
Total plant biomass	184.5 ± 18.8	454.8 ± 56.2	5.6 ± 0.5	7.6 ± 0.8	215.3 ± 29.1	306.7 ± 45.4	6.8 ± 1.0	7.0 ± 1.0	594.6 ± 63.9	747.7 ± 116.5	14.8 ± 1.7	14.8 ± 1.7	594.6 ± 63.9	747.7 ± 116.5
Percent from N-fixers	3.0%	11.7%	3.8%	17.4%	0.5%	7.9%	0.6%	9.3%	25.5%	28.1%	28.4%	28.4%	25.5%	28.1%
New plant biomass	353.3 ± 60.5	4.5 ± 1.0	4.5 ± 1.0	–	215.5 ± 48.6	4.1 ± 1.2	–	–	616.7 ± 143.7	–	–	–	–	–
Herbaceous biomass	67.8 ± 8.6	118.0 ± 13.6	2.3 ± 0.3	2.3 ± 0.3	82.3 ± 7.8	130.9 ± 14.2	2.5 ± 0.2	3.0 ± 0.3	210.5 ± 26.1	255.1 ± 37.2	5.6 ± 0.7	5.6 ± 0.7	210.5 ± 26.1	255.1 ± 37.2
Shrub biomass	105.2 ± 20.0	303.0 ± 59.9	3.0 ± 0.6	4.4 ± 0.8	115.1 ± 27.8	140.7 ± 39.1	3.8 ± 0.9	3.0 ± 0.9	324.4 ± 72.6	386.3 ± 115.9	7.6 ± 1.7	7.6 ± 1.7	324.4 ± 72.6	386.3 ± 115.9
New shrub biomass	199.3 ± 63.6	1.2 ± 7.7	1.2 ± 7.7	–	49.5 ± 42.6	0.1 ± 1.1	–	–	163.4 ± 149.2	–	–	–	–	–
Litter biomass	11.5 ± 2.5	33.7 ± 6.5	0.3 ± 0.1	0.9 ± 0.2	18.0 ± 2.4	35.1 ± 7.4	0.5 ± 0.1	1.0 ± 0.2	59.7 ± 9.2	106.4 ± 22.3	1.5 ± 0.2	1.5 ± 0.2	59.7 ± 9.2	106.4 ± 22.3
$N_{\min} - N_{\text{stored}}$	–	–	–4.1	–3.3	–	–	–5.3	–3.1	–	–	–	–	–	–11.5

Values are expressed in  $g\ m^{-2}$  growing season<sup>-1</sup> (1 SE) and are averaged for each of the burned watersheds. All aboveground biomass was considered new growth during the 2009–2010 growing season. New biomass in 2010–2011 was calculated as total plant biomass minus shrub biomass from the previous season.

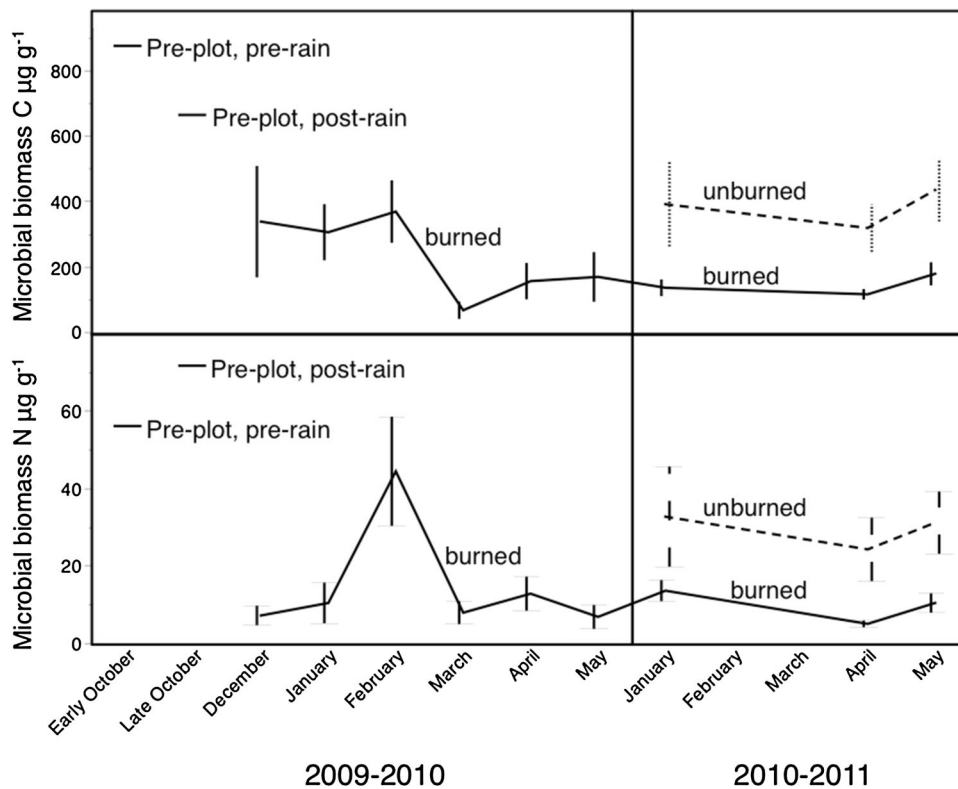


Figure 6. Monthly microbial biomass C and N in burned and unburned chaparral during the 2009–2010 and 2010–2011 growing seasons. Pre-plot microbial C and N are also shown.

### Controls over Soil N Cycling Following Fire

Fires rapidly release nutrients stored within plant tissues and promote ongoing nutrient mobilization (for example, enhanced N mineralization and nitrification; Raison 1979). Soil collected from burned areas prior to rain had high  $\text{NH}_4^+$  concentrations, driven by a combination of ash residues deposited on the soil surface and N mineralization that occurred during the dry season (Parker and Schimel 2011). In addition to  $\text{NH}_4^+$ , ash residues contain organic N, which can be mineralized upon soil wetting (Christensen and Muller 1975). These mechanisms likely contributed to the high  $\text{NH}_4^+$  concentrations we observed in burned areas in December and January of the 2009–2010 growing season (Figure 4).

Nitrification pulses also occurred during both growing seasons in burned chaparral, allowing  $\text{NO}_3^-$  to accumulate, while remaining low in unburned areas (Figures 4, 5). Low  $\text{NO}_3^-$  levels in unburned soils may result from either greater plant N uptake, reduced substrate supply (Vitousek 1982), microbial immobilization (Choromanska and DeLuca 2002), or some combination of these factors. For example, in soils supporting mature vegetation, mineralization, and some nitrification might occur, but rapid  $\text{NO}_3^-$  uptake may prevent it

from accumulating in the soil. On the other hand, if mature stands are more N limited than those that recently burned, plants might compete with nitrifying microorganisms for  $\text{NH}_4^+$ , thus slowing nitrification by limiting substrate supply (Fenn and others 1993). However, plant uptake and substrate supply may not be the only factors limiting nitrification in unburned areas. When total inorganic N concentrations were similar between burned and mature sites in the 2nd year of recovery, nitrification remained elevated in sites that had burned. This might have occurred because ash-induced fertilization in the first year stimulated nitrifier populations. Or, perhaps nitrification remained high because overall microbial biomass was suppressed, thereby reducing competition with heterotrophic microbes for  $\text{NH}_4^+$  (Choromanska and DeLuca 2002).

Following fire, C and nutrient inputs can stimulate microbial population growth, which might in turn enhance nutrient uptake and retention during the early stages of recovery while constraining nitrification (Knicker 2007). Microbial biomass was high after fire in preliminary sampling sites and plots, but decreased over the subsequent growing season to levels below those in unburned areas (Figure 6). The microbial biomass spike in burned areas corresponded with enhanced EOC and inor-

ganic N concentrations relative to those in areas that did not burn (Tables 3, 4). Thus, ash residues appear to have provided a flush of C and nutrients that may have stimulated microbial growth, but this was followed by a decline as resources were depleted. These results are similar to those found in grassland soils where soil bacterial populations increased more than twofold within 10 days after fire, followed by a crash at 30 days postfire (Grasso and others 1996).

The time required for soil microbial populations to recover from fire may be substantial, exceeding 10 years in coniferous forests (Fritze and others 1993), which typically do not burn as severely as chaparral (Hart and others 2005). In our study, 2 years after the Jesusita Fire and 3 years after the Tea Fire, microbial biomass had not recovered to values observed in unburned soils, suggesting that following an initial shortlived growth surge, microbial populations crash and remain low, at least during the first few years of recovery and perhaps until O-horizons recover, thereby replenishing labile C pools. It is possible that low microbial biomass would reinforce the vulnerability of chaparral soils to leaching and erosion, because smaller microbial populations cannot effectively immobilize N and/or aid in reforming soil aggregates that would physically stabilize soil (Knicker 2007). Additionally, if low heterotrophic biomass enhances nitrification, N might become even more prone to leaching.

Another factor that may be important in regulating nitrification in chaparral is soil pH (Hanan and others 2016; Ste-Marie and Paré 1999). Nitrification is generally acid sensitive (Castaldi and others 2008), yet fires tend to raise pH by consuming organic acids in soil organic matter (Kutiel and Inbar 1993) and depositing basic cations with ash (Giovannini and others 1990). These processes raise the solubility of organic matter, encouraging mineralization and increasing  $\text{NH}_4^+$  supply to nitrifiers (Raison 1979). Increases in pH also promote nitrifier activity by increasing the ratio of  $\text{NH}_3$  to  $\text{NH}_4^+$  in soil (Bååth and others 1995). In *A. fasciculatum* chaparral, near our study area, Christensen (1973) found pH to increase by 0.5 pH units following fire and suggested that this increase may be partially responsible for the  $\text{NO}_3^-$  accumulation he observed. We found that soil pH was less than 6.0 in unburned areas, and greater than 6.5 during the first January and February after fire (Figure 3). Although elevated pH did correspond with enhanced nitrification during the first few months of recovery, by the second year, pH had decreased to values observed in unburned soils (around 5.8), yet

nitrification rates remained high. Although pH may not be the proximal control on nitrification throughout recovery, it may have helped stimulate nitrifier activity immediately after fire, while other factors, such as substrate supply, might have helped sustain activity as soil pH decreased in the second year of study. Similar interactions have been observed in other systems such as the mixed hardwood forests in New England, where Likens and others (1970) found enhanced nitrification rates after clear-cutting, even as pH decreased from 5.1 to 4.3. Nitrification can, in fact, occur in acidic soils when  $\text{NH}_4^+$  concentrations are sufficiently high (De Boer and Kowalchuk 2001).

### Vegetation Recovery and N Immobilization

Because fires remove aboveground plant biomass, recovering chaparral ecosystems tend to be more leaky with respect to N than unburned chaparral (Coombs and Melack 2013; Gray and Schlesinger 1981). Ephemeral herbs play an important role in retaining N during the early stages of recovery, which is similar to the role of spring ephemeral species in northern hardwood forests that use soil resources each year prior to canopy closure (Zak and others 1990). In our study, postfire herbaceous plants, particularly *C. macrostegia*, took up available N so effectively that aboveground plant N accumulation exceeded measured soil net mineralization fluxes (Table 5). This discrepancy may result from several mechanisms, including inaccurate estimate of N availability with the net N-mineralization assay (Schimel and Bennett 2004), plants acquiring N from deeper in the soil profile, N in foliage of resprouting shrubs coming from stored N (DeSouza and others 1986), or even by excluding roots in the mineralization cores, inhibiting microbial priming (Kuzyakov and others 2000) that can sometimes stimulate N mineralization (Cheng and Kuzyakov 2005). Nevertheless, deficits were substantial in the first year.

Although N cycling appeared to be tight in burned plots,  $\text{NO}_3^-$  was still being exported to streams, at high rates immediately after fire, but declined rapidly over time (Coombs and Melack 2013; Verkaik and others 2013). However, higher early export does not necessarily contradict the concept of N limitation in our study area because xeric ecosystems intrinsically flush  $\text{NO}_3^-$  at the onset of winter rains (Austin and Vitousek 1998; Homyak and others 2014; Lewis and others 2006). If vegetation is N limited, plants may begin to assimilate N quickly, whereas in N saturated ecosystems, N export may continue through the

winter. Therefore, to evaluate whether chaparral ecosystems are N limited, it is better to focus on how rapidly N loss transitions to N retention (Homyak and others 2014).

## N Retention with Increasing Fire Frequency

Because more than 95% of the fires in chaparral are human-caused (Syphard and others 2007b), and because populations continue to grow, more frequent fires in the future may alter the long-term balance between N inputs and losses in these ecosystems. Although chaparral is resilient to fire rotation intervals ranging from 20 to 150 years (Syphard and others 2007a; Zedler 1995), N export can increase by orders of magnitude during the first storm events after fire (Coombs and Melack 2013; Verkaik and others 2013), before recovering plants gain access to ash-deposited nutrients. Fire also enhances the erosion of surface soils, where most nutrients are contained (Valeron and Meixner 2010). Therefore, shortened fire return intervals may enhance N loss over time. Such losses might gradually slow plant recovery and uptake, prompting a positive feedback on nutrient export. However, the extent to which increasing fire frequency slows recovery is likely a function of how N limited chaparral ecosystems are, which can vary over space and time.

## CONCLUSIONS

Fires destroy aboveground vegetation in chaparral, oxidizing large stores of nutrients and depositing ash that is rich in organic C, N, and mineral nutrients on soil surfaces. The extent to which surface erosion and leaching redistribute N down-slope is a function of the balance between the rates at which soil microbes metabolize N into forms that readily dissolve or leach (for example, dissolved organic N and  $\text{NO}_3^-$ ), and how rapidly recovering plants and microbes sequester this mobilized N.

Our results suggest that as ecosystems recover,  $\text{NO}_3^-$  production is regulated by multiple fine-scale factors, among which  $\text{NH}_4^+$  supply appears to be especially important. We found that the Tea and Jesusita Fires enhanced N turnover relative to rates in unburned stands. However, this was coupled with rapid plant growth, which likely helped to suppress leaching, while microbial biomass remained low. Hence, plant regrowth plays an important role in retaining N during the first few years of recovery from fire in chaparral, while microbial biomass does not.

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