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Carbon and nitrogen dynamics of pre- and post-fire chaparral exposed to varying atmospheric N deposition

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Abstract

Fire and atmospheric N deposition have the capacity to alter the N and C cycling and storage of semi-arid shrublands. Thus, we measured the pre- and post-fire soil and tissue C and N dynamics of three southern California chaparral stands exposed to varying levels of N deposition. Total soil N was positively correlated with N deposition exposure before and after fire, indicating that fire did little to alter patterns of soil N enrichment from atmospheric N deposition. Fire caused a significant increase in soil extractable N, and this increase was positively correlated with N deposition indicating that fire enhanced soil N availability more at sites exposed to high N deposition. Fire also caused the tissue N concentration of regenerating *Adenostoma fasciculatum* (chamise) shrubs to be significantly correlated with N deposition; however, the correlation was negative during the first year of fire recovery ($r^2 = 0.62$) and positive during the second ($r^2 = 0.94$) indicating complex and transient dynamics in shrub growth and N concentration. Overall, our results suggest that periodic fire in chaparral may not reduce the potential for N enrichment that develops over decades of N deposition and have important implications for the propensity of these semi-arid shrublands to become "N-saturated".

Keywords: *Adenostoma fasciculatum*; Biogeochemistry; *Ceanothus*; Chamise; Disturbance; Global change; Mediterranean-type ecosystems

1. Introduction

Anthropogenic N-deposition represents a significant input of N into many Mediterranean-type ecosystems such as the chaparral and coastal sage shrublands of southern California (Fenn et al., 2003a; Phoenix et al., 2006). High population density and reliance on automobile transportation lead to the development of large spatial gradients in gaseous and particulate N pollutants, the majority (85–95%) of which fall as dry deposition during the summer when inversion conditions trap these pollutants near the land surface (Bytnerowicz and Fenn, 1996; Fenn et al., 2003a). Annual inputs of atmospheric N to exposed urban shrublands are on the order of 25–50 kg N/ha (Bytnerowicz and Fenn, 1996; Fenn et al., 2003a; Riggan et al., 1985); however, the spatial pattern of N deposition is highly variable and poorly understood and sites at slightly higher elevations can receive up to 145 kg N/ha y (Fenn and Poth, 2004). These large inputs of N have

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the capacity to significantly alter the N and C storage and cycling of chaparral ecosystems, which are considered to be N-limited (Fenn et al., 2003b; Gray and Schlesinger, 1983; Kummerow et al., 1982). For example, atmospheric N inputs can increase total and available N through direct fertilization and enhanced mineralization, reduce soil and vegetation C:N ratios, enhance soil acidification, and promote losses of N from gaseous efflux and leaching (Fenn et al., 2003b; Meixner and Fenn, 2004; Michalski et al., 2004; Padgett et al., 1999; Riggan et al., 1985; Vourlitis et al., 2007a, b).

Superimposed on the regional N deposition regime is fire, which has an average return interval of 20–30 years (Keeley, 2000). The post-fire flora is dominated by herbaceous perennial and annual species that are replaced by shrubs within 4–5 years, and seeds of post-fire herbs, and many of the shrubs that replace them, require heat, smoke, and/or ash to germinate (Keeley, 2000). Fire consumes aboveground biomass, surface litter, and soil organic matter, which depending on intensity, causes losses in ecosystem N storage (DeBano and Conrad, 1978; DeBano et al., 1979), while other processes such as leaching, erosion, and/or runoff can cause additional and substantial losses of ecosystem N during the initial stages of chaparral succession (Gray and Schlesinger, 1981; Riggan et al., 1985, 1994). However, ash deposited from the charred remains of shrubs and litter is rapidly mineralized following fire causing a transient increase in available N, especially NH_4 (Carreira et al., 1994; Fenn et al., 1993; Riggan et al., 1985, 1994; Stock and Lewis, 1986). Furthermore, some plants and shrubs that re-colonize following fire are capable of symbiotic N fixation, which can add an additional 2–40 kg N/ha y to recovering chaparral (Ellis and Kummerow, 1989; Poth, 1982).

The interactions between N deposition and fire on chaparral soil and vegetation C and N dynamics are likely to be profound, but unfortunately are still highly uncertain (Fenn et al., 2003b; Lavorel et al., 1998). On the one hand, fire suppression has been blamed as a principal factor promoting "N-saturation," where atmospheric deposition causes N availability to exceed biotic demand leading to large losses of N (Fenn et al., 1998). Losses of N from periodic fire limit the accumulation of N in soil and vegetation (DeBano and Conrad, 1978; DeBano et al., 1979) and post-fire recovery promotes N sequestration in the biomass of regenerating shrubs (Rundel and Parsons, 1980). However, burning also promotes N input from symbiotic N fixation (Ellis and Kummerow, 1989; Kummerow et al., 1978; Poth, 1982), so potential losses of N from combustion may be rapidly offset by input from N fixation. Furthermore, the magnitude of N enrichment has the capacity to alter disturbance dynamics by affecting the frequency, intensity, and/or trajectory of post-fire recovery (Minnich and Dezzani, 1998).

Southern Californian chaparral shrublands are a mosaic of different-aged stands (Minnich, 1983) that are subjected to varying levels of atmospheric N deposition (Bytnerowicz and Fenn, 1996; Fenn et al., 2003a; Riggan et al., 1985). Given the potential for fire and N deposition to alter ecosystem C and N cycling and storage dynamics, understanding the interaction between fire and atmospheric N deposition is a critical research priority (Fenn et al., 2003b; Lavorel et al., 1998), especially immediately after fire when changes in soil and plant N storage and cycling are most rapid (Black, 1987; DeBano and Conrad, 1978; DeBano et al., 1979; Fenn et al., 1993; Gray and Schlesinger, 1981; Keeley, 2000; Riggan et al., 1985, 1994). To assess this interaction, we conducted a case study where vegetation and soil C and N was quantified before and after fire in three southern California chaparral stands exposed to varying levels of N deposition.

2. Methods

2.1. Site descriptions

Pre- and post-fire observations of plant and soil C and N were conducted at the Sky Oaks Field Station (SOFS), San Dimas Experimental Forest (SDEF), and the San Bernardino National Forest (SBNF) (Table 1), which are located across a N deposition gradient in southern California (Fenn et al., 2003a; Tonnesen et al., 2002). The stands were composed of mature chaparral vegetation prior to fire, and while each stand burned on a different date, all of the stands burned within a 13-month period between September 2002 and October 2003 (Table 1). Unfortunately, fire intensity was not measured but qualitative estimates may be derived by observing changes in soil N and C immediately after fire (DeBano and Conrad, 1978; DeBano et al., 1979).

SOFS is located 1418 m above sea level (asl) in NE San Diego County, California, and is dominated by the evergreen shrub *Adenostoma fasciculatum* H & A (commonly known as chamise) (Table 1). The site is on a

Table 1
Location and properties of the research sites

Variable	Sky Oaks Field Station (SOFS)	San Bernardino National Forest (SBNF)	San Dimas Experimental Forest (SDEF)
Latitude:longitude	33°21′N:116°34′W	34°19′N:117°18′W	34°10′N:117°44′W
N deposition (kg N/ha y)	8.1	11.9	18.4
Elevation (m)	1418	807	451
Rainfall (cm)	57	56	44
Soil texture (% sand, silt, clay)	78, 14, 8	78, 5, 17	70, 14, 16
Soil nomenclature	Ultic haploxeroll	Typic xerorthent	Typic xerorthent
Bulk density (g/cm^3)	1.34	1.28	1.26
Dominant species[a]	*Af, Cg, Qd, As*	*Af, Cc*	*Af, Cc, Qd*
Slope/aspect (°/SE–SW)	4–10	4–10	4–12
Month/year of fire	July 2003	October 2003	September 2002

Rainfall data are from the Western Regional Climate Center (www.wrcc.dri.edu, verified 29 March 2007) for locales near the study sites and represent >50-year averages (Vourlitis et al., 2007a, b). Data for soil bulk density and texture are for the upper 0–10 cm soil layer. N-deposition estimates depict total (wet + dry) deposition derived from the high-resolution Community Multiscale Air Quality (CMAQ) N deposition model (Tonnesen et al., 2002).

[a] *Af*, *Adenostoma fasciculatum*; *As*, *Adenostoma sparsifolium*; *Qd*, *Quercus dumosa*; *Cg*, *Ceanothus greggii*; *Cc*, *Ceanothus crassifolius*.

4–10° slope with a SE–SW aspect and receives on average 57 cm of rainfall per year. Annual wet + dry N deposition derived from the high-resolution (4 km^2) community multiscale air quality (CMAQ) N deposition model (Tonnesen et al., 2002) is estimated to be 8.1 kg N/ha (Table 1). The stand was 50 years old when it burned in July 2003. Prior to the fire, shrubs were on average 1 m tall, shrub cover was 0.83 m^2/m^2, and density was 1.3 shrubs/m^2, while 8 months after fire average shrub height was 0.2 m, cover was 0.02 m^2/m^2, and density was 0.7 shrubs/m^2 (Fig. 1). *A. fasciculatum* re-sprouts were present as soon as 2 months post-fire while herbaceous "fire-followers" and large numbers of *Ceanothus greggii* A. Gray appeared shortly after the spring rains in 2004. Soil is an Ultic Haploxeroll derived of micaceous schist (Moreno and Oechel, 1992) with a sandy loam texture and a bulk density of 1.34 g/cm^3 (Table 1).

SBNF is located 807 m asl in the San Bernardino Mountains of San Bernardino County, California, and is also chamise-dominated chaparral (Table 1). The site is situated on a 4–10° slope with a SE–SW aspect that receives on average 11.9 kg N/ha and 56 cm of rainfall annually. The site was 35 years old when it burned in October 2003. Prior to fire, the stand was relatively open and composed of ca. 2 m tall shrubs, while 8 months post fire, average shrub height was 0.5 m, cover was 0.2 m^2/m^2, and a density was 7.2 shrubs/m^2 (Fig. 1). *A. fasciculatum* and *Ceanothus crassifolius* Torr. were the dominant post-fire shrubs. Soil is a Typic xerorthent of the Cieneba–Tollhouse Series derived of schist and granite (USDA, 1980) with a sandy loam texture and a bulk density 1.28 g/cm^3.

SDEF is an *A. fasciculatum*-dominated chaparral located 451 m asl in the San Gabriel Mountains of Los Angeles County, California. The site receives approximately 44 cm of rainfall annually and is situated on a 4–12° slope with a SE–SW aspect. Annual wet + dry N deposition is estimated to be 18.4 kg N/ha (Table 1). The stand was 42 years old prior to fire in September 2002 and was a dense thicket of shrubs that reached a maximum height of 3 m. Approximately, 1 year after fire, *A. fasciculatum* and *C. crassifolius* were the dominant shrubs, average shrub height and cover was 0.7 m and 0.4 m^2/m^2, respectively, and shrub density was 2.5 shrubs/m^2 (Fig. 1). Soil is a Typic Xerorthent derived of gneiss and schist (Dunn et al., 1988) with a sandy loam texture and a bulk density of 1.26 g/cm^3 (Table 1).

2.2. Field sampling and chemical analysis

Soil, tissue, and litter samples at each site were collected within four-10 × 10 m plots. Field sampling was conducted between September 2002 and September 2005, and samples were obtained seasonally (March, June, September, and December) to coincide with the seasonal variation in rainfall. However, each site burned at a

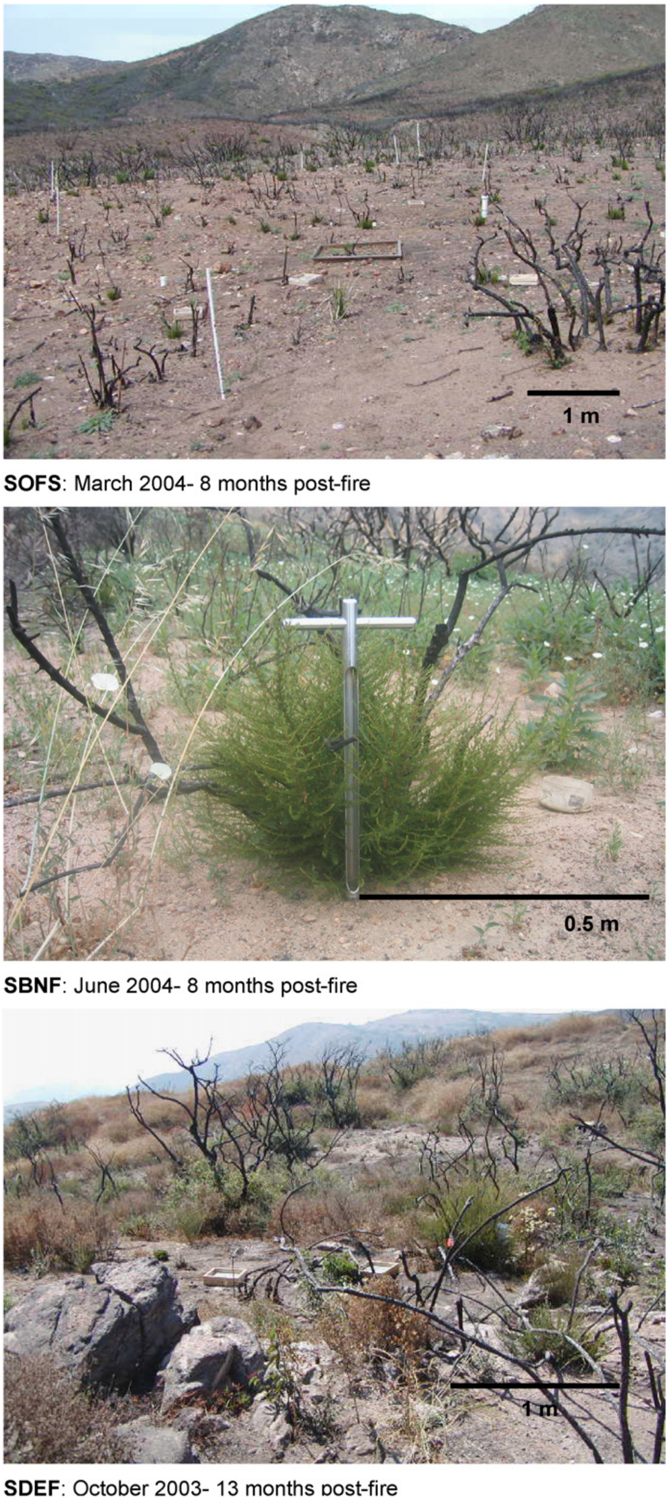

Fig. 1. Images of regenerating *Adenostoma fasciculatum* at the Sky Oaks Field Station (SOFS), approximately 8 months post-fire; the San Bernardino National Forest (SBNF), approximately 8 months post-fire; and the San Dimas Experimental Forest (SDEF) approximately, 13 months post-fire. The black horizontal lines in the bottom right-hand-corner of each panel depict the scale of the image. For additional information regarding scale, the wooden litterfall traps in the images for SOFS and SDEF (the small light-colored spares in the center of the images) are 25×25 cm in area and 5 cm tall and the metal "T-bar" at SBNF is approximately 50 cm tall. Note the lack of herbaceous cover at SOFS and the copious herbaceous cover at SBNF and SDEF.

Table 2
Sample dates and the number of months before (negative values) and after fire (positive values) for the Sky Oaks Field Station (SOFS), San Bernardino National Forest (SBNF), and San Dimas Experimental Forest (SDEF) study sites

Recovery interval	SOFS		SDEF		SBNF	
	Months before or after fire	Month/year	Months before or after fire	Month/year	Months before or after fire	Month/year
Pre-fire	−10	September 2002	0	September 2002		
	−7	January 2003			−10	January 2003
	−4	April 2003			−7	April 2003
	−1	June 2003			−4	June 2003
1 year post-fire	3	October 2003	12	October 2003	3	January 2004
	6	January 2004			6	March 2004
	9	March 2004			9	June 2004
	12	June 2004			12	September 2004
2 years post-fire	15	September 2004	15	January 2004	15	December 2004
	18	December 2004	18	March 2004	18	March 2005
	21	March 2005	21	June 2004	21	June 2005
	24	June 2005	24	September 2004	24	October 2005

Fire occurred in July 2003 at SOFS, October 2003 at SBNF, and September 2002 at SDEF. Sample dates are rounded to the nearest month.

different time leading to an unbalanced number of pre-fire sampling campaigns (Table 2). For example, SOFS and SBNF were sampled four and three times, respectively, before fire while SDEF was sampled only once because the stand burned about 1 week after our field sampling campaign. Fire damaged research infrastructure and extensive erosion during the first year of stand recovery limited access to the sites causing unavoidable gaps in data. For example, SOFS and SBNF could not be sampled for 3 months after fire while SDEF could not be sampled for nearly 12 months after fire. Thus, when possible, each site was sampled every 3 months providing data before and after fire (Table 2).

Soil samples were obtained from the surface (0–10 cm) using a 4.7 cm diameter × 10 cm deep (173.5 cm^3) bucket auger or a 1.8 cm diameter × 10 cm deep (25.5 cm^3) T-bar at 2–4 randomly chosen points in each plot. Samples were transferred from the core sampler to a polyethylene sample bag and immediately returned to the lab and stored at 4 °C until analysis for extractable NH_4 and NO_3 and total N and C content (Robertson et al., 1999).

Soil extractable NO_3 and NH_4 was determined 1–4 days after sample collection. Ten grams of fresh soil were added to 40 ml of 2 M KCl and continuously agitated on a reciprocating shaker for 1 h (Mulvaney, 1996). The supernatant was filtered using a 0.45 μm syringe filter and the NH_4 (Hofer, 2001) and NO_3 (Knepel, 2001) concentration of the extract was measured using an auto-analyzer (Quikchem 3000, Lachat Instruments, Milwaukee, WI, USA). Soil pH was measured 1–4 days after sample collection. Fifteen grams of fresh soil was added to 30 ml DI-water and pH was measured after 30 min using a standard pH meter (MP 220, Mettler-Toledo, Columbus, OH, USA).

Tissue samples consisting of 10–15 cm long live apical shoots were collected seasonally from chamise shrubs at 2–4 random points per plot. Tissue samples at each random point were pooled per plot, dried at 70 °C for 1 week, and ground to a fine powder. Analysis of total N and C and the $\delta^{15}N$ natural abundance was conducted at the Kansas State University Stable Isotope Mass Spectrometry Laboratory using a coupled CHN-mass spectrometer.

Average aboveground biomass of regenerating chamise shrubs was estimated at each site using dimensional analysis (Bonham, 1989). Measurements were conducted 12 and 24 months after fire at SOFS and SBNF and 15 and 24 months after fire at SDEF. Each shrub rooted within a 2 m radius (12.56 m^2) sub-plot located in the center of each main-plot was measured for height (H) and average diameter (D), which was calculated from measurements made along the widest axis and the perpendicular axis. Shrub volume (V) was calculated as area ($\pi[D^2/4]$) times H, and aboveground biomass was calculated from V using a linear regression equation that was calibrated from previously harvested shrubs ($n = 10$ shrubs; $r^2 = 0.99$). Estimates of aboveground biomass prior to fire were only available for SOFS.

2.3. Statistical analysis and derived quantities

The average monthly rate of aboveground biomass production and N uptake were estimated for 0–12 months and 12–24 months after fire for SOFS and SBNF and 0–15 months and 15–24 months after fire for SDEF. Estimates of aboveground shrub biomass and tissue N concentration were assumed to be zero immediately after fire, which is a reasonable assumption given that all live aboveground biomass was consumed by fire. The average monthly rate of aboveground biomass production during each interval was calculated as the change in biomass divided by the elapsed time and expressed as g dry weight/shrub month. The average monthly rate of N uptake was calculated similarly except that N content per shrub (g N/shrub) was substituted for biomass, and expressed as g N/shrub month. Biomass production and N uptake were expressed on a per shrub basis, as opposed to a per unit area basis, because we were interested in quantifying the relative growth and N uptake rates of recovering chamise shrubs across the N deposition gradient.

Soil and shrub C and N response variables were summarized for periods up to 1 year before fire (pre-fire) and 1 and 2 years after fire (post-fire) by calculating the average ($\pm$se; $n = 4$) value for a given pre- and post-fire period. As mentioned above, differences in fire date and post-fire damage between sites resulted in an unbalanced sampling intensity before and up to 1 year after fire (Table 2), and it was not possible to calculate annual averages during these periods from observations obtained during comparable seasons. The effect of this unbalanced sampling on the calculated pre- and post-fire (1 year) averages is presumably more important for variables that exhibit a seasonal trend. Differences in soil and vegetation N and C response variables were assessed using repeated-measures ANOVA with site and time as fixed effects. Trends in soil and vegetation N and C response variables as a function of N deposition derived from the CMAQ deposition model (Tonnesen et al., 2002) were assessed using linear regression for pre- and post-fire periods. Analyses were conducted using NCSS 2004 (Hintze, 2004) and data violating assumptions of normality and homoscedasticity were LN-transformed prior to analysis (Zar, 1984).

3. Results and discussion

3.1. Soil extractable N and pH

Extractable $NO_3 + NH_4$ in the surface mineral soil (0–10 cm) varied significantly over time and between sites and there was a significant site–time interaction. Extractable NO_3 (Fig. 2a) and NH_4 (Fig. 2c) exhibited mild seasonal variation and tended to peak during the fall and winter when dry deposition is at a seasonal maximum (Padgett et al., 1999). Prior to fire, soil extractable NO_3 varied between 1.6 and 3.0 μg N/g (Fig. 2b) and NH_4 varied between 1.2 and 2.0 μg N/g (Fig. 2d) and soil extractable N was not significantly correlated with N deposition exposure (Table 3). One year after fire, the concentration of soil extractable NO_3 and NH_4 increased more than 2-fold for SOFS and 4-fold for SBNF, but for SDEF, the increase in soil extractable NO_3 and NH_4 was 10- and 21-fold, respectively, and the increase in soil extractable NO_3 and NH_4 was positively related to N deposition exposure (Table 3). Two years post fire, soil extractable NO_3 and NH_4 had returned to pre-fire levels at SOFS but were still more than 2-fold higher at SBNF and 6–17 times higher at SDEF compared to pre-fire levels, and soil extractable N was positively correlated with N deposition exposure (Table 3).

These results suggest that fire enhanced the concentration of extractable N at all sites presumably because N was rapidly mineralized from decomposing surface ash (Carreira et al., 1994; Fenn et al., 1993; Stock and Lewis, 1986). Furthermore, the magnitude of the post-fire increase in both soil extractable NO_3 and NH_4 was positively correlated with N deposition exposure (Table 3), suggesting that mineralization of ash- and/or N-rich debris was enhanced by N deposition. Increases in N mineralization are expected at sites exposed to high N deposition because N enrichment causes a decline in the C:N ratio of litter and soil organic matter (Korontzi et al., 2000; Vourlitis and Zorba, 2007; Vourlitis et al., 2007c). Another potential avenue of N enrichment is direct fertilization (Michalski et al., 2004); however, if this avenue was important for the sites

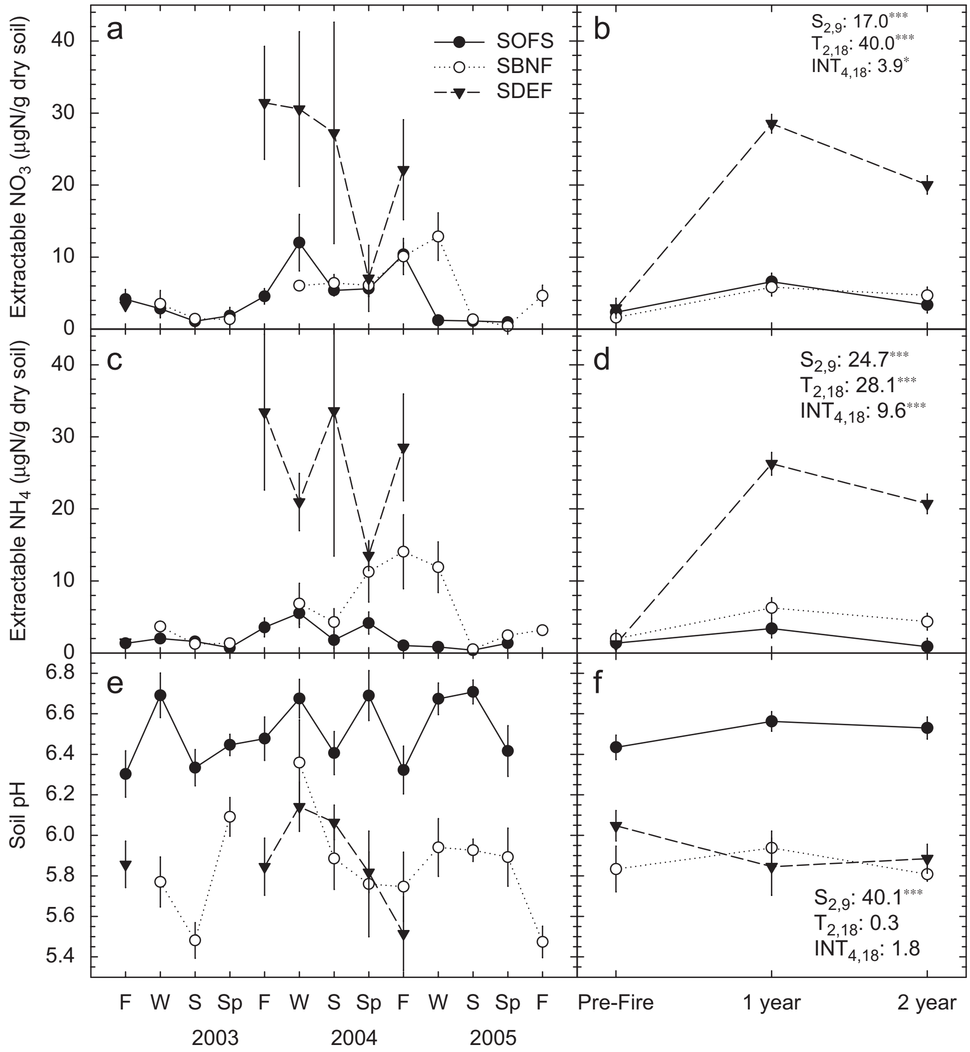

Fig. 2. Mean ($\pm$S.E.; $n = 4$ plots per site) soil extractable NO_3 (a, b), NH_4 (c, d), and pH (e, f) for surface (0–10 cm) soil at the Sky Oaks Field Station (SOFS), San Bernardino National Forest (SBNF), and the San Dimas Experimental Forest (SDEF). Data are displayed as a function of the season and year that samples were obtained (panels a, c, and e) and as averages before and after fire (panels b, d, and f). Also shown are the results from a repeated-measures ANOVA (*F*-statistic, degrees of freedom, and *p*-value) with site (*S*), time (*T*), and the site–time interaction (INT) as fixed effects for data summarized during pre- and post-fire intervals. $^{*}p<0.05$; $^{**}p<0.01$; $^{***}p<0.001$.

observed here then soil extractable N would have also been positively correlated with N deposition exposure prior to fire, which was not observed (Table 3). There is also no compelling evidence to indicate that other factors, such as variations in fire intensity (DeBano and Conrad, 1978; DeBano et al., 1979) and/or the recruitment of "fire-following" plants capable of symbiotic N fixation (Ellis and Kummerow, 1989; Kummerow et al., 1978; Poth, 1982), contributed to the positive correlation observed between post-fire N availability and N deposition exposure. For example, if the magnitude of soil N and C loss increases linearly with fire intensity (DeBano and Conrad, 1978; DeBano et al., 1979), then post-fire trends in the magnitude of soil N and C loss (Fig. 3b and d) suggest that fire intensity was highest at SDEF and SOFS and lowest at SBNF, which is not well correlated to N deposition exposure (Table 1). Similarly, the abundance of the principal symbiotic N-fixing plant species (*Ceanothus greggii*, *C. crassifolius*, and/or *Lotus scoparius*) in the post-fire community was not significantly correlated with N deposition exposure (S. Pasquini, CSUSM, unpublished data).

Table 3
Linear regression statistics including the intercept, slope, and coefficient of variation (R^2) for soil and tissue C- and N-dependent variables before fire and 1 and 2 years after fire as a function of estimated N deposition derived from the high-resolution Community Multiscale Air Quality (CMAQ) N deposition model (Tonnesen et al., 2002)

Dependent variable	Units	Before fire			1 year after fire			2 years after fire		
		Intercept	Slope	R^2	Intercept	Slope	R^2	Intercept	Slope	R^2
Soil extractable NO_3[a]	μg/g	1.5	0.091	0.07	**−17.7**	**2.543**	**0.58**	**−13.9**	**1.866**	**0.69**
Soil extractable NH_4[a]	μg/g	1.7	−0.003	0.01	**−23.5**	**2.998**	**0.55**	**−20.1**	**2.338**	**0.58**
pH		6.5	−0.030	0.19	**6.9**	**−0.063**	**0.56**	**6.8**	**−0.054**	**0.47**
Total soil N	%	**0.002**	**0.006**	**0.57**	**0.006**	**0.005**	**0.55**	**0.019**	**0.004**	**0.58**
Total soil C	%	1.2	0.004	0.01	1.4	−0.015	0.05	1.0	0.015	0.05
Soil C:N ratio		**34.9**	**−1.278**	**0.74**	**39.9**	**−1.536**	**0.84**	22.1	−0.390	0.20
Tissue N	%	1.2	0.011	0.10	**2.8**	**−0.085**	**0.62**	**0.1**	**0.095**	**0.94**
Tissue C	%	52.1	−0.190	0.12	46.8	0.164	0.09	**53.3**	**−0.303**	**0.92**
Tissue C:N ratio		46.9	−0.673	0.20	**11.6**	**1.863**	**0.83**	**87.2**	**−3.059**	**0.97**
Biomass production[a]	g/shrub month	ND	ND	ND	**−2.0**	**0.327**	**0.59**	4.9	−0.108	0.13
N uptake[a]	g/shrub month	ND	ND	ND	**0.2**	**0.359**	**0.73**	9.4	−0.270	0.28
Soil $\delta^{15}N$	‰	1.6	0.019	0.02	0.3	0.033	0.04	**3.1**	**−0.125**	**0.43**
Tissue $\delta^{15}N$	‰	**−4.6**	**0.196**	**0.58**	−1.8	0.051	0.17	−0.8	−0.001	0.01
Enrichment (ε)	‰	**−6.3**	**0.179**	**0.50**	−2.1	0.017	0.02	**−4.2**	**0.158**	**0.57**

Bold values depict a regression that is significantly different from zero ($p<0.05$). Regression degrees of freedom = 1, 10 (n = 4 per site). ND, no data.
[a]LN-transformed to meet assumptions of regression.

Soil pH also showed a mild seasonal trend with peaks in the fall and winter (Fig. 2e). When averaged over pre- and post-fire intervals, soil pH was significantly different between sites but did not change significantly over time indicating that fire had little effect on soil pH (Fig. 2f). Sites exposed to high N deposition (SBNF and SDEF) had significantly lower surface soil pH than SOFS, and soil pH was significantly negatively correlated with N deposition exposure after fire but not before (Table 3). Regardless, sites exposed to higher levels of N deposition (SBNF and SDEF) had substantially lower soil pH before and after fire (Fig. 2e and f) indicating that long-term exposure to N deposition causes soil acidification that is not alleviated by fire. Chronic N deposition has been observed to promote soil acidification because N deposition stimulates N cycling processes such as nitrification and leaching (Fenn et al., 1996; Korontzi et al., 2000).

3.2. Soil N and C

Total soil N content varied significantly between sites but not over time, and seasonal trends were highly variable (Fig. 3a and b). Regardless of fire, SDEF consistently had the highest total soil N followed by SBNF and SOFS. Both SDEF and SOFS exhibited slight declines in soil N during the first year post fire while soil N levels for SBNF exhibited a relatively consistent increase in soil N over time (Fig. 3b). In contrast, total soil C was not significantly different between sites or over time (Fig. 3c and d). The variable response of soil N and C to fire is in contrast to other studies that reported significant post-fire declines in both soil N and C (DeBano and Conrad, 1978; DeBano et al., 1979; Dunn et al., 1979; Rundell, 1983). However, while the intensity of the fires is unknown, the initial decline in soil N and C at SOFS and SDEF suggest that fire intensity may have been higher at these sites (DeBano and Conrad, 1978; DeBano et al., 1979). Pre- and post-fire differences in total soil N were positively correlated with N deposition exposure while differences in soil C were independent of N deposition exposure (Table 3). The significant and consistently positive trend between soil N and atmospheric N exposure (Table 3) indicates that long-term N deposition substantially increased soil N storage (Fenn et al., 2003b; Vourlitis et al., 2007a, b) and that the resulting N enrichment may not be reduced by fire.

The soil C:N ratio varied little over season time scales (Fig. 3e); however, there was a significant difference between sites and there was a significant site–time interaction indicating complex dynamics in soil C:N (Fig. 3f). The soil C:N ratio was negatively correlated with N deposition exposure before and 1 year after fire,

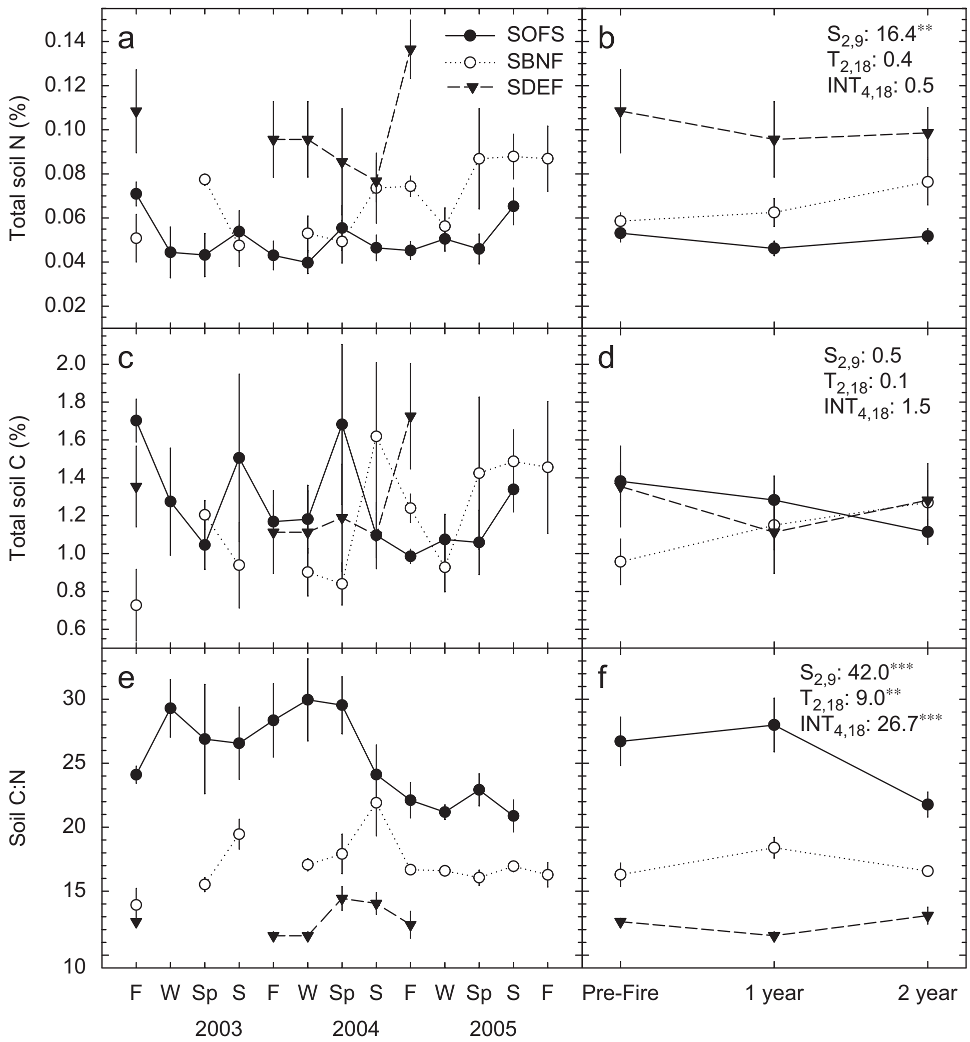

Fig. 3. Mean (±S.E.; $n = 4$ plots per site) total N (a, b) and C (c, d) concentration and the C/N ratio (e, f) for surface (0–10 cm) soil at the Sky Oaks Field Station (SOFS), San Bernardino National Forest (SBNF), and the San Dimas Experimental Forest (SDEF). Data are displayed as a function of the season and year that samples were obtained (panels a, c, and e) and as averages before and after fire (panels b, d, and f). Also shown are the results from a repeated-measures ANOVA (*F*-statistic, degrees of freedom, and *p*-value) with site (*S*), time (*T*), and the site–time interaction (INT) as fixed effects for data summarized during pre- and post-fire intervals. $^{*}p<0.05$; $^{**}p<0.01$; $^{***}p<0.001$.

which is consistent with results reported for several ecosystems exposed to enhanced N deposition (Fenn et al., 2003b; Vourlitis et al., 2007a, b), but after 2 years of recovery, the soil C:N was no longer correlated with N deposition. Longer-term fluctuations in soil C and N storage are likely over the course of secondary succession because of variations in physical environmental characteristics (Hastings et al., 1989) and plant and soil properties, such as plant growth and nutrient uptake (Black, 1987; Neary et al., 1999), soil organic matter and litter decomposition (Dunn et al., 1979; Fenn et al., 2003a, b), plant species composition (Keeley, 2000), and N losses from leaching or gaseous efflux (Riggan et al., 1994).

3.3. Tissue N and C

The tissue N concentration of chamise shrubs varied substantially over seasonal and annual time scales and increased during the spring and summer for all sites, especially in 2004 (Fig. 4a). When averaged over pre- and

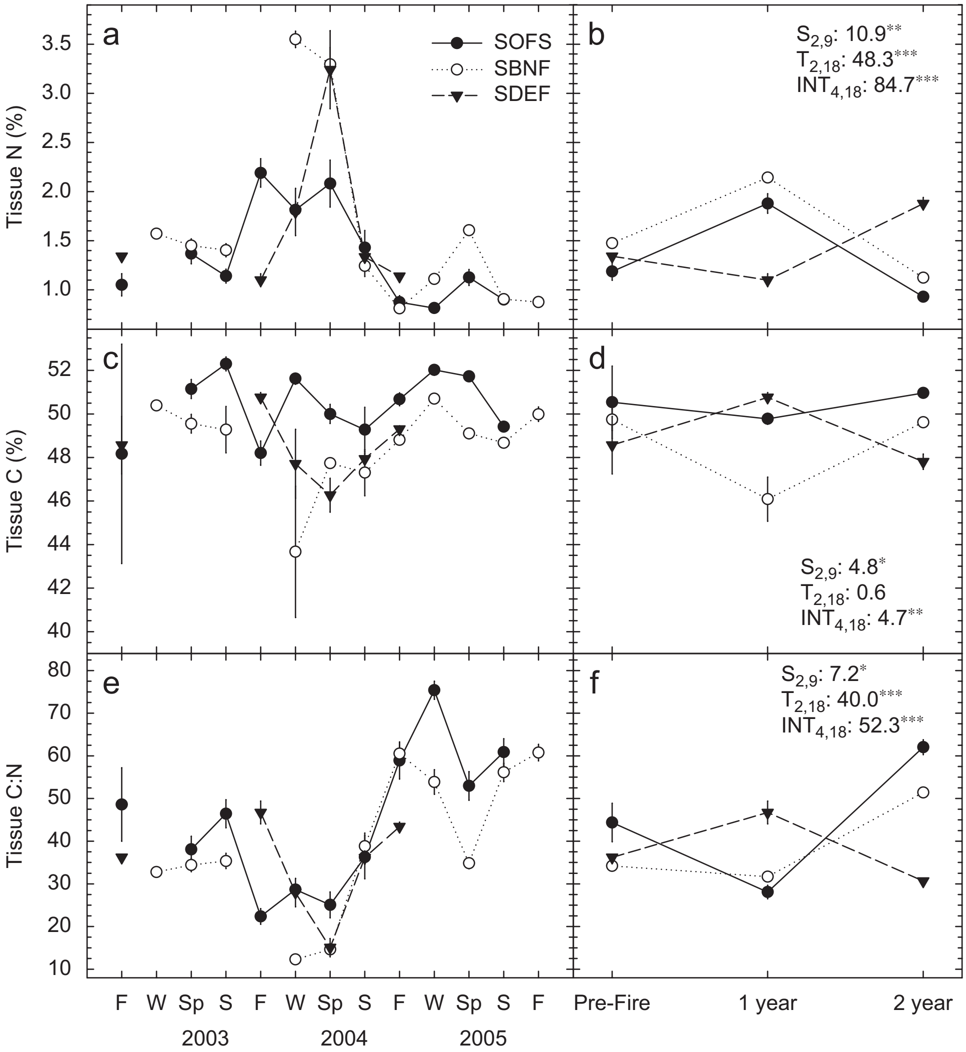

Fig. 4. Mean (±S.E.; $n = 4$ plots per site) total N (a, b) and C (c, d) concentration and the C/N ratio (e, f) for *Adenostoma fasciculatum* shrubs at the Sky Oaks Field Station (SOFS), San Bernardino National Forest (SBNF), and the San Dimas Experimental Forest (SDEF). Data are displayed as a function of the season and year that samples were obtained (panels a, c, and e) and as averages before and after fire (panels b, d, and f). Also shown are the results from a repeated-measures ANOVA (*F*-statistic, degrees of freedom, and *p*-value) with site (*S*), time (*T*), and the site–time interaction (INT) as fixed effects for data summarized during pre- and post-fire intervals. $^{*}p<0.05$; $^{**}p<0.01$; $^{***}p<0.001$.

post-fire time intervals, tissue N and C concentration varied significantly between sites and there was a significant site–time interaction (Fig. 4b and d). Tissue N prior to fire varied between 1.2% and 1.5% and was highest at SBNF and lowest at SOFS. One year after fire the tissue N concentration increased by 0.65% for SOFS and SBNF but decreased by 0.2% for SDEF, and tissue N concentration was significantly negatively correlated with N deposition exposure (Table 3). At the same time, the tissue C concentration for shrubs at SOFS and SBNF either declined or remained unchanged, while tissue C for shrubs at SDEF increased (Fig. 4d), suggesting that shrubs at SDEF were diluting internal N reserves (Rundel and Parsons, 1980). However, 2 years post fire the patterns of tissue C and N were reversed. For SOFS and SBNF, tissue C concentration increased while tissue N declined, but for SDEF, tissue N increased while tissue C declined (Fig. 4b and d). At the end of the study period, tissue N was significantly positively correlated while tissue C was significantly negatively correlated with N deposition exposure (Table 3). Thus, while N exposure led to tissue N enrichment, it did not enhance tissue C storage at least after 2 years of post-fire shrub recovery.

Tissue C:N ratios were typically lowest in the spring and summer, especially in 2004 (Fig. 4e), and when averaged over pre- and post-fire intervals, tissue C:N varied significantly in response to N deposition exposure and time since fire and there was a significant site–time interaction (Fig. 4f). Prior to fire, chamise growing at SOFS had the highest C:N ratio (45 g C/g N) while shrubs growing at SBNF and SDEF had a C:N of 36 and 38 g C/g N, respectively. One year after fire, tissue C:N varied between 46 g C/g N (SDEF) and 28 g C/g N (SOFS) and was positively correlated with N deposition, indicating that C storage per unit N was positively correlated with N deposition exposure (Asner et al., 1997). However, after 2 years of recovery, tissue C:N varied between 63 g C/g N (SOFS) and 30 g C/g N (SDEF) and was significantly negatively correlated with N deposition (Table 3), indicating that N-induced increases in shrub C storage per unit N during the immediate stages of post-fire succession were transient.

3.4. Biomass production and N uptake

Shrub biomass production increased rapidly after fire (Fig. 5a), and both the biomass production and N uptake (Fig. 5b) were significantly positively correlated with N deposition exposure during the first year of post-fire recovery (Table 3). Chamise shrubs at SDEF produced on average four times (SBNF) and 50 times (SOFS) more aboveground biomass during the first year of recovery (Fig. 5a). However, while individual chamise shrubs were larger at SDEF and SBNF, there was no statistically significant difference in aboveground standing crop (g/m^2) because chamise density was inversely proportional to mean shrub biomass (S. Pasquini, CSUSM, unpublished data). During the second year of recovery, the mean biomass and N uptake of chamise shrubs at SOFS and SBNF increased, while the mean biomass and N uptake of shrubs at

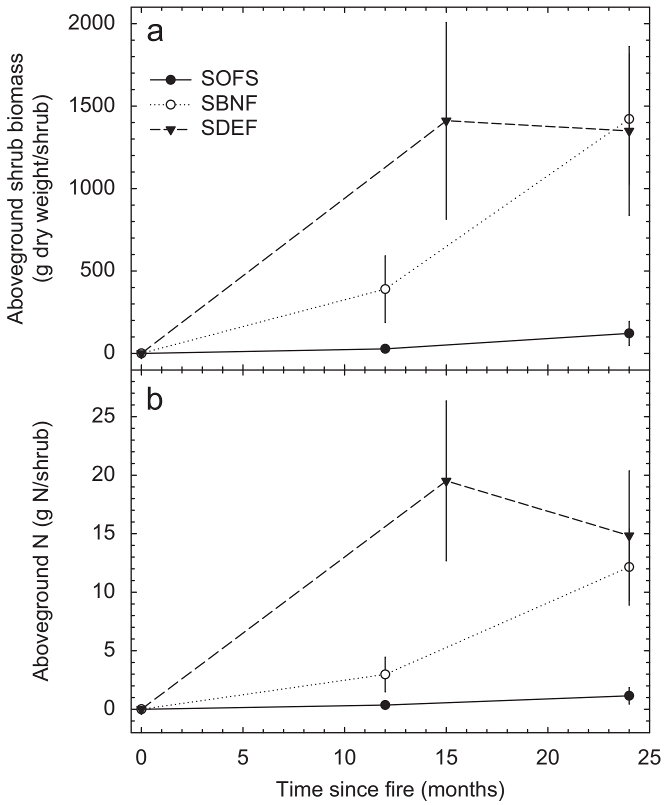

Fig. 5. Mean (±S.E.; $n = 4$ plots per site) aboveground biomass production (a) and N content (b) for *Adenostoma fasciculatum* shrubs at the Sky Oaks Field Station (SOFS), San Bernardino National Forest (SBNF), and the San Dimas Experimental Forest (SDEF) up to 12 (SOFS and SBNF) and 15 (SDEF) months post-fire (a, b) and between 12–24 (SOFS) and 15–24 (SDEF) post-fire (c, d).

SDEF declined slightly (Fig. 5), and spatial patterns of biomass production and N uptake were no longer linearly related to N deposition exposure (Table 3).

The differences in post-fire shrub growth observed between sites is presumably due to spatial variations in N deposition exposure; however, other factors such as historical differences in resource allocation to belowground structures (Sparks et al., 1993), limitations in other soil resources such as P or water (Kummerow et al., 1982; Moreno and Oechel, 1992), and/or differences in microclimatic conditions during stand recovery may also be important. Chamise re-sprouts from fire (Sparks et al., 1993) and shrubs that survived fire were rapidly re-sprouting 3–4 months after fire at SOFS and SBNF, and presumably, SDEF. Although soil C and N data suggest a relatively more intense fire at SOFS and SDEF (Fig. 3b and d), there did not appear to be any differences in shrub mortality between sites that would indicate large differences in fire intensity, and hence, stand recovery. Rather, variations in rainfall and temperature between the study sites may in part explain some of the variation in post-fire shrub growth, especially during the first year of stand recovery. Weather records for locales close to the study sites indicate that rainfall during the October–May wet season at SDEF was 10 cm higher than at SBFN and 19 cm higher than at SOFS, while minimum monthly temperatures at the high-elevation SOFS site (8.8 °C) were 2–4 °C lower that that observed for SBNF (10.6 °C) and SDEF (12.6 °C). Thus, warmer and wetter conditions, coupled with high N availability (Fig. 2b and d), may have stimulated shrub biomass production relatively more at SDEF during the first year of post-fire recovery than at the other study sites.

3.5. Soil and tissue $\delta^{15}N$ natural abundance

Soil $\delta^{15}N$ natural abundance did not exhibit any obvious seasonal trend but was substantially lower in 2004 (Fig. 6a). When averaged over pre- and post-fire intervals soil $\delta^{15}N$ varied significantly between sites and over time and there was a significant site–time interaction (Fig. 6b). In general, soil $\delta^{15}N$ declined at each site 1 year after fire presumably because surface soils were covered with ash that is depleted in ^{15}N relative to bulk soil (Högberg, 1997). By 2 years post-fire SOFS and SBNF soils became enriched in ^{15}N by 1.6 and 0.6‰, respectively, while the $\delta^{15}N$ of SDEF soil remained unchanged (Fig. 6b). Surface soil enrichment may be expected over time as fresh litter accumulates from regenerating shrubs, which tend to acquire N from deeper soil reserves that are enriched in ^{15}N (Högberg, 1997). Furthermore, leaching losses of N, which are high in regenerating chaparral stands (Riggan et al., 1985, 1994), can also cause soil ^{15}N enrichment (Emmett et al., 1998; Högberg, 1991). Soil $\delta^{15}N$ natural abundance was not significantly correlated with N deposition exposure prior to fire or 1 year post fire but was significantly negatively correlated with N deposition exposure 2 years post fire ($r^2 = 0.43$; Table 3). Typically N deposition increases soil $\delta^{15}N$ in mature ecosystems because N input stimulates processes that discriminate against ^{15}N (Johannisson and Högberg, 1994; Korontzi et al., 2000); however, it is likely that variations in N cycling, plant growth and allocation, and community composition during succession will cause patterns of soil $\delta^{15}N$ to differ between disturbed and mature ecosystems (Högberg, 1997).

Tissue $\delta^{15}N$ natural abundance failed to show any obvious seasonal trends (Fig. 6c) but varied significantly between sites and over time since fire and there was a significant site–time interaction (Fig. 6d). Prior to fire, the tissue $\delta^{15}N$ of chamise varied between −3.3‰ for SOFS and −1.2‰ for SDEF and tissue $\delta^{15}N$ was positively correlated with N deposition exposure (Table 3), which is consistent with results reported for southern California coniferous forests exposed to chronic atmospheric N deposition (Korontzi et al., 2000). Shrubs growing at all sites became either slightly (SBNF and SDEF) or strongly (SOFS) enriched in ^{15}N during the first year post fire, which may indicate that shrubs were accessing N from deeper in the soil profile (Högberg, 1997) and/or that recovering shrubs were translocating stored N to growth sinks (Evans, 2001). Relative enrichment in tissue ^{15}N continued up to 2 years post fire (Fig. 6d); however, the magnitude of enrichment was substantially less than observed up to 1 year post fire. Tissue $\delta^{15}N$ natural abundance was correlated with N deposition exposure prior to fire but not after (Table 3) presumably because fire altered the $\delta^{15}N$ of the source N (Högberg, 1997).

An enrichment factor (ε) was developed by Mariotti et al. (1981) to quantify the isotope fractionation when a N source ($\delta^{15}N_s$) is transformed into a N product ($\delta^{15}N_p$) in a closed system. In turn, ε may be indicative of the kinetics of N cycling because many processes, such as mineralization, nitrification, and/or leaching

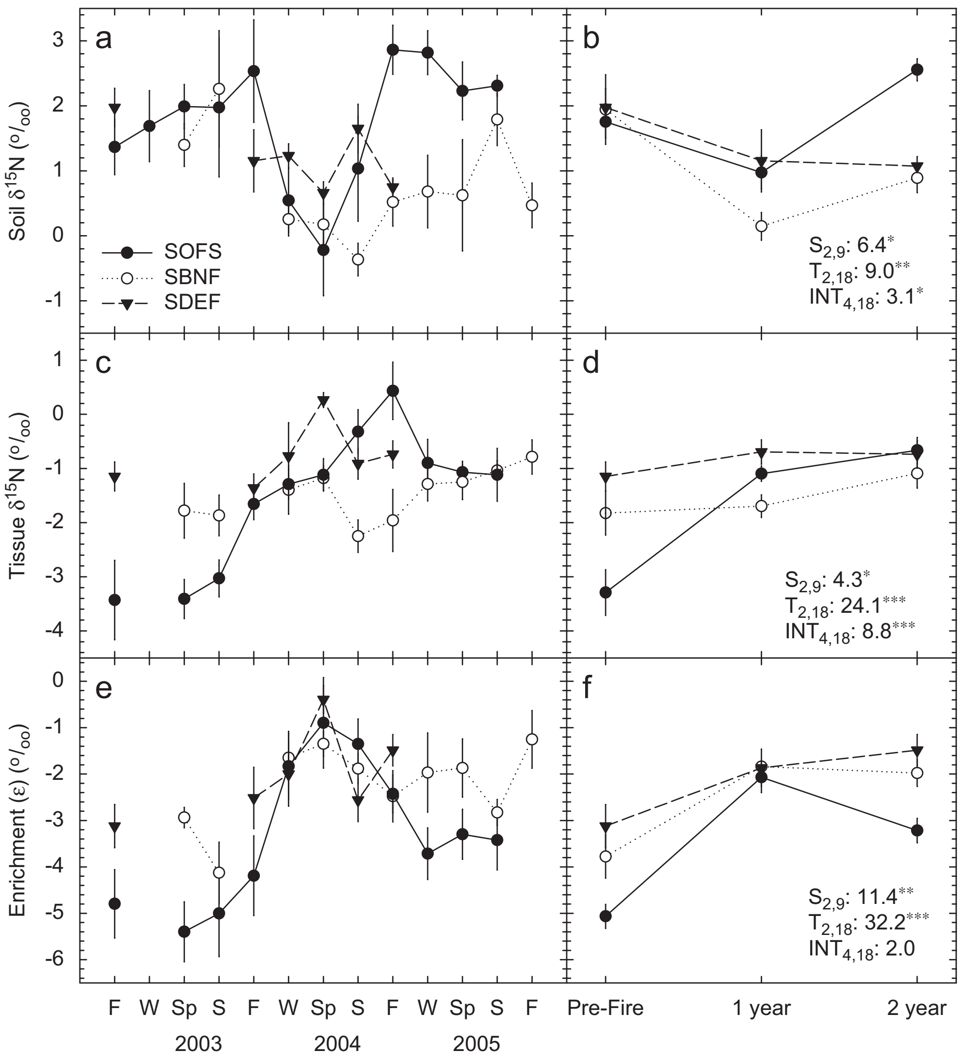

Fig. 6. Mean ($\pm$S.E.; $n = 4$ plots per site) δ^{15}N natural abundance for surface soil (a, b), *Adenostoma fasciculatum* shrubs (c, d), and the enrichment factor (ε) calculated as the difference between tissue and soil δ^{15}N natural abundance (e, f) at the Sky Oaks Field Station (SOFS), San Bernardino National Forest (SBNF), and the San Dimas Experimental Forest (SDEF). Data are displayed as a function of the season and year that samples were obtained (panels a, c, and e) and as averages before and after fire (panels b, d, and f). Also shown are the results from a repeated-measures ANOVA (*F*-statistic, degrees of freedom, and *p*-value) with site (*S*), time (*T*), and the site–time interaction (INT) as fixed effects for data summarized during pre- and post-fire intervals. $^{*}p<0.05$; $^{**}p<0.01$; $^{***}p<0.001$.

discriminate against ^{15}N (Johannisson and Högberg, 1994; Korontzi et al., 2000). Emmett et al. (1998) have used ε to quantify the magnitude of ^{15}N enrichment where local variations in soil and tissue δ^{15}N natural abundance can potentially confound variations caused by other sources such as N deposition. Using this rationale, ε was calculated as the difference between the product ($\delta^{15}N_{tissue}$) and substrate ($\delta^{15}N_{soil}$) to determine the ^{15}N enrichment in response to fire and exogenous N. ε did not show any obvious seasonal trend (Fig. 6e) but varied significantly as a function of site and time since fire and there was a significant site–time interaction (Fig. 6f). Prior to fire, ε varied between -5.1‰ for SOFS and -3.1‰ for SDEF (Fig. 6f), indicating significantly higher ^{15}N enrichment at SDEF, and ε was significantly positively related to N deposition (Table 3). One year after fire, all sites had a similar ε that was on average -2‰, and there was no significant relationship between ε and N deposition (Table 3). Thus, fire lead to substantial ^{15}N enrichment at all sites presumably in response to enhanced N mineralization and leaching (Carreira et al., 1994; Fenn et al., 1993; Riggan et al., 1994). Two years post fire, ε declined by 1‰ for SOFS and remained unchanged for SDEF and SBFN (Fig. 6f), and ε was again positively related to N deposition (Table 3).

4. Conclusions

Vegetation and soil C and N were quantified before and after fire in three southern California chaparral stands exposed to different levels of atmospheric N deposition. While an unbalanced sampling effort before and after fire (Table 2) and small number of field sites may obscure interactions between fire and N deposition exposure, our data suggest that many of the N and C variables investigated were substantially altered by fire and significantly correlated with N deposition exposure before and/or after fire. Fire modified soil extractable N (Fig. 2), the soil C:N ratio (Fig. 3f), tissue N concentration and the C:N ratio (Fig. 4), aboveground biomass production (Fig. 5), and the δ^{15}N natural abundance (Fig. 6); however, many of these fire-induced modifications were transient. The consistent positive trend between N deposition and total soil N regardless of fire suggests that N enrichment resulting from atmospheric N deposition will not be alleviated by periodic fire. Shrub growth and N accumulation were positively correlated with N deposition only during the first year of fire recovery, suggesting that N accumulation in shrub biomass is only transiently increased in sites exposed to N deposition, and hence, not likely to alleviate potential soil N enrichment. These results have important implications for the structure and function of chaparral shrublands and the propensity for these shrublands to become N saturated under current and future N deposition and fire regimes.

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