Published in final edited form as:

J Arid Environ. 2010 February ; 74(2): 310–314. doi:10.1016/j.jaridenv.2009.08.013.

Post-fire primary production and plant community dynamics in chaparral stands exposed to varying levels of nitrogen deposition

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Abstract

High levels of atmospheric nitrogen (N) deposition to southern California chaparral shrublands may interact with fire to affect biomass production and plant species composition during secondary succession. To determine the potential interactions between post fire recovery and N deposition we compared rates of aboveground net primary production (ANPP), shrub growth, and the relative abundance of *Adenostoma fasciculatum*, other sub-dominant shrubs, and herbaceous species of three chaparral stands exposed to different levels of atmospheric N deposition over the first 3 years of post-fire succession. Our data suggest that rates of ANPP ($\text{gdw m}^{-2} \text{ month}^{-1}$) and aboveground N storage ($\text{gN m}^{-2} \text{ month}^{-1}$) for these chaparral stands were not related to N deposition even though sites exposed to high levels of N deposition had significantly higher rates of shrub growth ($\text{gdw plant}^{-1} \text{ month}^{-1}$) and N uptake ($\text{gN plant}^{-1} \text{ month}^{-1}$). However, high-N stands were composed of larger shrubs with a lower density, and this trade-off between shrub size and density may explain the low correlation between N deposition and post-fire ANPP. Differences in relative plant species abundance between sites were significantly correlated with N deposition exposure, where stands exposed to high N deposition had a lower relative abundance of *A. fasciculatum* and a higher relative abundance of other shrub and herbaceous species. While many factors can affect rates and patterns of post-fire recovery, these results suggest that chronic exposure to N deposition may significantly alter plant growth and species composition in successional chaparral stands.

Key words and phrases

Adenostoma fasciculatum; air pollution; *Ceanothus crassifolius*; *Ceanothus greggii*; disturbance; Mediterranean-type ecosystems; semi-arid shrublands; secondary succession

1. Introduction

Atmospheric nitrogen (N) deposition is a chronic problem in many urban areas, especially in southern California where urban shrublands can receive inputs of $20\text{--}45 \text{ kgN ha}^{-1} \text{ y}^{-1}$ (Fenn

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et al. 2003). Previous studies indicate that the growth of some chaparral shrubs, such as *Adenostoma fasciculatum*, is N limited (McMaster et al. 1982); however, the growth of other shrubs, such as *Ceanothus* sp. and *Lotus scoparius*, may not be limited by N availability because of symbiotic N-fixation (Kummerow et al. 1978; Virginia and Delwiche 1982). In contrast, the growth of many herbaceous species may be highly responsive to exogenous N (Padgett and Allen 1999). Such variable responses of chaparral shrubs and herbaceous vegetation to anthropogenic N deposition have the capacity to influence primary production and community composition (Westman 1981; Bobbink et al. 1991; Zavaleta et al. 2003; Vourlitis and Pasquini 2009).

The effects of N deposition may interact with fire, which is an important agent of disturbance in southern Californian chaparral (Hanes 1971). Fire can alter N availability and pool size depending on intensity (Neary et al. 1999), and substantial N loss from volatilization and leaching can follow high intensity fires (DeBano and Conrad 1978), especially in areas impacted by high atmospheric N deposition (Riggan et al. 1994). However, Vourlitis and Pasquini (2008) found that total soil N for sites exposed to high N deposition for decades had been 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. In addition, fire enhanced soil N availability more at sites exposed to high N deposition. Overall, these results suggest that periodic fire in chaparral may not reduce the potential for N enrichment that develops over decades (Vourlitis and Pasquini 2008). These results have important implications for the productivity and community composition of chaparral stands recovering from fire.

To determine the potential interactions between post-fire recovery and N deposition we measured the biomass production and relative plant species abundance of three chaparral sites exposed to different levels of atmospheric N deposition. These stands burned during wildfires that occurred within a 13-month period, and although potential differences in the fire regime and site characteristics may obscure the effects of N deposition, we hypothesized that post-fire rates of aboveground net primary production (ANPP), shrub growth, and differences in plant species relative abundance would be correlated with N deposition exposure.

2. Materials and methods

Research was conducted at the Sky Oaks Field Station (SOFS), San Dimas Experimental Forest (SDEF) and the San Bernardino National Forest (SBNF), which burned between September 2002 and October 2003. Field sampling was conducted seasonally (March, June, September, and December) within four-10 × 10 m plots at each site between December 2004, when the SOFS, SBNF, and SDEF sites were 5, 2, and 15 months post-fire, respectively, and September 2006, when the SOFS, SBNF, and SDEF sites were 38, 35, and 48 months post-fire, respectively.

Site characteristics are displayed in Table 1 and were discussed in detail by Vourlitis and Pasquini (2008). Climate data were not available for the research sites and were compiled from Western Regional Climate Center archives (www.wrcc.dri.edu) for sites that were near the field sites. For SOFS, data was compiled from Ranchita (1274 m above sea level (asl)) located 21 km SSE from the study site. Data for SBNF were averaged from Lake Arrowhead (1584 m asl) and Redlands (402 m asl) located 4 km NW and 2 km SSW from the study site, respectively. Data for SDEF were averaged from Pasadena (262 m asl) and Tanbark Flat (862 m asl) located 23 km W and 7 km NNE from the study site, respectively.

Gravimetric soil moisture was measured from soil (4–8 samples/plot) obtained from the upper 10 cm soil layer using a bucket auger. Percent gravimetric soil water was calculated as $[(M_f - M_d) / M_d] * 100$ where M_f was the fresh mass of soil and M_d was the mass of soil after drying at 105°C.

All plants ≥ 20 cm in height were counted and measured for height and width within a 2 m radius (12.57 m²) quadrat located in the center of each 10 × 10 m plot, while plants < 20 cm in height were counted and measured for height and width within a 0.5 × 0.5 m (0.25 m²) quadrat centered in the middle of each 12.57 m² quadrat. The volume of each plant was calculated as the product of canopy area (A) and maximum height, where $A = \pi D^2 / 4$ and D is the average shrub diameter calculated from measurements of the maximum and perpendicular diameter (Bonham 1989). Aboveground biomass (g dry weight (gdw)) was calculated as a function of plant volume using regression equations (LN-biomass vs. LN-volume) that were developed for each species from previously harvested individuals ($n = 18$ –26 individuals per species; coefficients of determination varied between 0.95–0.99, Vourlitis et al. 2009). In seasons when herbaceous annuals and grasses were too abundant to count, a bulk harvest was used to determine herbaceous biomass.

Tissue samples consisting of 10–15 cm long live apical shoots were collected from all dominant shrub species (2–4 samples/species/plot). Tissue samples were pooled by species in each plot, dried at 70°C, and ground to a fine powder. Total tissue N was quantified by dry combustion using a CHN analyzer (ECS 4010, Costech Analytical Technologies, Inc., Valencia, CA, USA).

Total aboveground biomass per unit area (gdw/m²) was calculated as the sum of the total aboveground shrub and herbaceous biomass in each plot divided by plot area. Average shrub biomass (gdw/shrub) was calculated as the average biomass of each shrub species per plot, and shrub density (shrubs/m²) was calculated as the sum of all individuals per species divided by plot area. Aboveground shrub N pool size (gN/m²) was calculated as the product of aboveground shrub biomass (gdw/m²) and the tissue N concentration, while shrub N content (gN/shrub) was calculated as the product of average shrub biomass (gdw/shrub) and the tissue N concentration.

The relative abundance of *Adenostoma fasciculatum* (the dominant shrub at all sites), “other shrubs” (such as *Ceanothus greggii* and *Trichostema parishii* at SOFS, *C. crassifolius* and *Eriodictyon trichocalyx* at SBNF, and *C. crassifolius* and *Quercus durata* at SDEF), and herbaceous plants (annual and perennial forbs and grasses) was quantified as the proportion of the total biomass that was accounted for by each species group.

Rates of net primary production, shrub growth, and N uptake and storage dynamics over the 3 year study period were calculated using linear regression with time since fire (months) as the independent variable and a given biomass or N variable as the dependent variable. For example, the rate of total aboveground net primary production (ANPP_t; gdw m⁻² month⁻¹) was calculated with total aboveground biomass (gdw/m²) as the dependent variable, while net shrub primary production (ANPP_s) and net herbaceous primary production (ANPP_h) were calculated with total aboveground shrub biomass and total herbaceous biomass, respectively as dependent variables. Similarly, the average shrub growth rate (gdw shrub⁻¹ month⁻¹) was calculated with average shrub biomass as the dependent variable, while the average shrub N uptake rate (gN shrub⁻¹ month⁻¹) and the rate aboveground N storage in shrub biomass (gN m⁻² month⁻¹) were calculated with shrub N content and aboveground shrub N pool size, respectively as dependent variables. Biomass and N content were assumed to be zero immediately after fire and regressions were forced through the origin. Differences in regression slopes between sites were tested using curve-inequality

randomization tests. The effects of N deposition exposure on ANPP, shrub N storage, shrub growth and N uptake rates, and relative abundance were analyzed using linear regression with estimated N deposition rates (Table 1) as the independent variable. All statistical analyses were performed using NCSS (version 2004, Kaysville, Utah, USA).

3. Results

Rainfall patterns in 2003 were similar for all sites except in September when nearly 120 mm of rainfall fell at SOFS from monsoonal storms (Fig. 1a). Larger differences in rainfall were observed in November 2004–March 2005, when SBNF and SDEF experienced 300–400 mm more rainfall than SOFS. At this time the SDEF stand was 24–28 months post-fire while the SOFS and SBNF stands were 15–18 and 12–15 months post-fire, respectively. Small differences in average monthly temperature were observed between the sites (Fig. 1b); however, SDEF had warmer winter temperatures than SOFS and SBNF probably owing to the lower elevation of SDEF (Table 1). SOFS and SDEF had similar gravimetric soil moisture in the upper 10 cm soil layer, which ranged between 2–3% during the summer months to as high as 15% during the winter rainy season, while SBNF had substantially (4–10%) lower surface soil moisture than SOFS and SDEF during the winter and spring growing seasons (Fig. 1c).

Post-fire rates of $ANPP_t$ and $ANPP_s$ were significantly higher at SBNF than at SOFS or SDEF, while the rate of $ANPP_h$ was statistically similar at all sites (Table 2), and site differences in ANPP were not significantly correlated with N deposition exposure (Table 3). In contrast, the average shrub growth and N uptake rates were significantly higher at SDEF and SBNF than at SOFS (Table 2), and both rates were significantly positively correlated with estimated N deposition (Table 3). Average shrub density for the 3-year study period was significantly negatively correlated with N deposition exposure (Table 3).

There was a significant decline in the relative abundance of *A. fasciculatum* and a significant increase in the relative abundance of “other shrubs” and herbaceous plants as a function of N deposition 2 and 3 years post-fire when biomass data was available from all sites (Table 3). *A. fasciculatum* accounted for 83% of the total biomass at SOFS, 79% at SBNF, and 47% of the total biomass at SDEF (Fig. 3). Other shrubs accounted for 11% (SOFS), 20% (SBNF), and 36% (SDEF) of the total aboveground biomass, while the relative abundance of herbaceous plants was < 20% at all sites; however, SDEF had a larger proportional biomass (17%) than SOFS and SDEF (Fig. 3).

4. Discussion and conclusions

The poor correlation between N deposition and $ANPP_t$, $ANPP_s$, or $ANPP_h$ is contrary to our hypothesis and may have been due to differences in fire intensity and/or climate during stand recovery. Each stand burned during a different wildfire, and variation in fire intensity can affect the growth and germination response of recovering shrubs (Moreno and Oechel 1991, 1992; Keeley 2000); however, Vourlitis and Pasquini (2008) found that soil C and N decreased at SOFS and SDEF but increased at SBNF immediately after fire, suggesting that fire intensity was higher at SOFS and SDEF (DeBano and Conrad 1978). Thus, the higher ANPP at SBNF may have been due in part to lower fire intensity, which would be expected to lower fire-induced shrub and seed mortality, increase rates of post-fire germination, and/or cause a reduction in volatile nutrient losses (DeBano and Conrad 1978; Moreno and Oechel 1991, 1992; Neary et al. 1999; Keeley 2000). In contrast, the potential for confounding effects of climate differences on ANPP are less straightforward. For example, SBNF and SDEF had similar precipitation during the study period but the rate of $ANPP_t$ and $ANPP_s$ was significantly different for these sites, while SBNF had the highest rate of ANPP

but the lowest soil water content of all of the study sites. The lack of a statistically significant relationship between ANPP_h and N deposition is surprising given that herbaceous plants are often more responsive to N addition (Padgett and Allen 1999). However, herbaceous biomass production at these sites was substantially more spatially and temporally variable than shrub biomass production (Pasquini 2008), which undoubtedly complicated the estimation of a linear trend over the 3 year study period.

While estimates of ANPP were not related to N deposition exposure, the average shrub growth and N uptake rates were significantly positively correlated with N deposition exposure (Table 3). However, sites exposed to higher levels of N deposition also had lower density, suggesting a trade-off between shrub density and size. This trade-off between shrub size and density presumably explains in part why differences in ANPP were not related to N deposition.

Post-fire trends in the relative abundance of *A. fasciculatum*, “other shrubs,” and herbaceous plants indicate differences in community composition that were significantly correlated with N deposition (Table 3). The relative abundance of herbaceous plants was positively correlated with high N deposition, which is consistent with research in N-enriched southern California coastal sage shrublands (Minnich and Dezzani 1998; Padgett and Allen 1999; Sirulnik et al. 2007). In contrast, the decline in *A. fasciculatum* relative abundance suggests that N deposition exposure may have inhibited the production of *A. fasciculatum*. Previous studies found that the growth of *A. fasciculatum* is N limited (McMaster et al. 1982), thus an increase in N deposition would be expected to increase the growth and relative abundance of *A. fasciculatum*. However, N deposition can also lead to soil acidification (Fenn et al. 1996; Korontzi et al. 2000; Vourlitis and Pasquini 2008), which can inhibit the growth and survival of shrubs (Roem et al. 2002). Species differences in growth and abundance would also change the dynamics of interspecific interactions, such as resource competition, but unfortunately potential changes in these dynamics cannot be addressed with the data provided.

In conclusion, we found that post-fire trends in total community, shrub, and herbaceous biomass production were not related to N deposition exposure even though the average growth rate and N uptake of shrubs was positively correlated with N deposition. Sites exposed to higher atmospheric N input had larger shrubs but lower shrub density, and this trade-off between shrub size and density in part caused community biomass production to be independent of N deposition exposure. Sites exposed to higher levels of N deposition had a lower relative abundance of *A. fasciculatum* and a higher abundance of other shrubs and herbaceous species, indicating a shift in community composition along the N-deposition gradient. While these trends indicate important changes in early-successional community structure in response to N deposition exposure the mechanism for these changes is still poorly understood. Even so, our results indicate significant changes in post-fire shrub growth and recovery along a N deposition gradient that suggest potentially large variations in chaparral structure and function as succession proceeds.

Acknowledgments

This research was made possible in part by funding by the NSF-CAREER (DEB-0133259) and NIH-NIGMS-SCORE (S06 GM 59833) programs. Special thanks to all the many undergraduate, graduate students and others that helped with biomass measurements, without them, this study would not have been possible. Thank you to the SDSU Field Station Programs for use of the Sky Oaks Field Station and to Mike Oxford and the US Forest Service for use of the San Dimas Experimental Forest.

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Fig. 1.

(a) Total monthly rainfall and (b) mean monthly temperature for locates close to the study sites. Climate data were compiled from the Western Regional Climate Center (www.wrcc.dri.edu) archives for Ranchita, CA (SOFS), Lake Arrowhead, CA and Redlands, CA (SBNF), and Pasadena, CA and Tanbark Flat, CA (SDEF). (c) The mean ($\pm$ se; $n = 4$) surface soil moisture (0–10 cm) for the Sky Oaks Field Station (SOFS; black-circles, solid lines), the San Bernardino National Forest (SBNF; open-circles, dashed lines), and the San Dimas Experimental Forest (SDEF; black-triangles, dotted-lines).

Fig. 2. Mean ($\pm$ se; $n = 4$ plots per site) percent contribution of *Adenostoma fasciculatum* (Top panel), other shrubs (middle panel), and herbaceous plant species (bottom panel) to the total biomass for the Sky Oaks Field Station (SOFS; black-circles, solid lines), San Bernardino National Forest (SBNF; open-circles, dotted-lines), and the San Dimas Experimental Forest (SDEF; black-triangles, dashed lines) over the first 3 years of post-fire recovery.

Table 1

Characteristics and locations of the study sites. Total nitrogen deposition (wet + dry) was estimated from a high-resolution nitrogen deposition model (Tonnesen et al. 2007). Precipitation and air temperature data are mean ($\pm$ sd) annual averages during the study period for locations near the study sites. Data for soil texture and bulk density are for the upper 0–10 cm soil layer (Vourlitis and Pasquini 2008).

Characteristic	Sky Oaks Field Station	San Bernardino National Forest	San Dimas Experimental Forest
Latitude and longitude (N:W)	33°21':116°34'	34°19':117°18'	34°10':117°44'
Nitrogen deposition (kg N ha ⁻¹ y ⁻¹)	8.1	11.9	18.4
Elevation (m)	1418	807	451
Mean ($\pm$ sd) annual precipitation (mm)	471 $\pm$ 206	603 $\pm$ 398	852 $\pm$ 693
Mean ($\pm$ sd) annual temperature (°C)	14.8 $\pm$ 0.5	13.9 $\pm$ 0.7	17.8 $\pm$ 0.5
Sand, Silt, Clay (%)	78, 14, 8	78, 16, 6	71, 17, 11
Soil texture class	Sandy loam	Sandy loam	Sandy loam
Soil nomenclature	Ultic haploxeroll	Typic xerorthent	Typic xerorthent
Bulk Density (g cm ⁻³)	1.34	1.28	1.26
Dominant species [†]	<i>Af</i> , <i>Cg</i>	<i>Af</i> , <i>Cc</i> , <i>Dr</i> , <i>Et</i>	<i>Af</i> , <i>Cc</i>
Species richness	39	15	16
Slope/aspect	4–10°/SE-SW	4–10°/SE-SW	4–12°/SE-SSW
Month/year of fire	July 2003	October 2003	September 2002

[†] *Af* = *Adenostoma fasciculatum*; *Cg* = *Ceanothus greggii*; *Cc* = *Ceanothus crassifolius*; *Dr* = *Dendromecon rigida*; *Et* = *Eriodictyon trichocalyx*

Table 2

The mean ($\pm$ 95% confidence interval; $n = 4$ plots per site) rate total aboveground net primary production ($ANPP_t$), total aboveground net shrub primary production ($ANPP_s$), total aboveground net herbaceous primary production ($ANPP_h$), aboveground shrub N storage, average shrub growth rate, and the average shrub N uptake rate for the Sky Oaks Field Station (SOFS), San Bernardino National Forest (SBNF), and San Dimas Experimental Forest (SDEF) study sites. Rates of change in $ANPP$, average shrub growth, shrub N storage, and N uptake were calculated using linear regression with regressions forced through the origin to assume zero biomass and N content immediately after fire. Data for SOFS correspond to a 30 month period between December 2005 (5 months post-fire) and July 2006 (35 months post-fire). Data for SBNF correspond to a 33 month period between December 2004 (2 months post-fire) and September 2006 (35 months post-fire). Data for SDEF correspond to a 21 month period between December 2004 (15 months post-fire) and September 2006 (36 months post-fire). Shown is the slope of the regression ($\pm$ 95% CI), and differences between slopes were tested using curve inequality randomization tests. Slopes within each row with a different lower-cases letter are significantly different ($p < 0.05$).

Variable	Units	Mean $\pm$ 95% CI		
		SOFS	SBNF	SDEF
$ANPP_t$	gdw $m^{-2} month^{-1}$	17.3 $\pm$ 2.0 ^a	33.8 $\pm$ 7.0 ^b	19.1 $\pm$ 5.7 ^a
$ANPP_s$	gdw $m^{-2} month^{-1}$	16.8 $\pm$ 2.3 ^a	33.6 $\pm$ 7.2 ^b	15.8 $\pm$ 4.5 ^a
$ANPP_h$	gdw $m^{-2} month^{-1}$	0.52 $\pm$ 0.72 ^a	0.27 $\pm$ 0.28 ^a	3.30 $\pm$ 3.86 ^a
Aboveground shrub N storage	gN $m^{-2} month^{-1}$	0.13 $\pm$ 0.02 ^a	0.32 $\pm$ 0.07 ^b	0.18 $\pm$ 0.05 ^a
Average shrub growth rate	gdw shrub ⁻¹ $month^{-1}$	4.2 $\pm$ 1.1 ^a	8.7 $\pm$ 1.9 ^{ab}	13.2 $\pm$ 3.5 ^b
Average shrub N uptake rate	gN shrub ⁻¹ $month^{-1}$	0.03 $\pm$ 0.02 ^a	0.09 $\pm$ 0.03 ^{ab}	0.15 $\pm$ 0.02 ^b

Table 3

Linear regression results between estimated N deposition exposure (independent variable) and several dependant variables including the rate total aboveground net primary production (ANPP_t), total aboveground net shrub primary production (ANPP_s), total aboveground net herbaceous primary production (ANPP_h), aboveground shrub N storage, average shrub growth rate, average shrub N uptake rate, and the average relative abundance of *Adenostoma fasciculatum*, “other shrubs,” and herbaceous plants during the second and third year of post-fire recovery. Shown is the linear regression equation, coefficient of determination (r^2), F-statistic and degrees of freedom (regression,error), and the probability of type-1 error (p-value).

Dependent variable	Equation [†]	r^2	F _{1,10}	p-value
ANPP _t	NA	0.05	0.6	>0.05
ANPP _s	NA	0.07	0.7	>0.05
ANPP _h	NA	0.13	1.5	>0.05
Aboveground shrub N storage	NA	<0.01	0.1	>0.05
Average shrub growth rate	$y = 1.10N - 4.57$	0.50	10.0	0.01
Average shrub N uptake rate	$y = 0.01N - 0.07$	0.65	18.2	0.002
Density	$y = 8.87 - 0.38N$	0.47	8.8	0.014
<i>Adenostoma fasciculatum</i>	$y = 1.16 - 0.04N$	0.62	16.6	0.002
Other shrubs	$y = 0.02N - 0.08$	0.47	8.9	0.014
Herbaceous plants	$y = 0.01N - 0.09$	0.45	8.2	0.017

[†] Linear equations are only presented for statistically significant models. NA = $p > 0.05$. y = the dependent variable and N = estimated N deposition exposure.