Experimental dry-season N deposition alters species composition in southern Californian mediterranean-type shrublands

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Abstract. Nitrogen (N) deposition in heavily polluted southern Californian shrublands is estimated to be 20–45 kg N ha⁻¹ yr⁻¹, but more exposed locales can receive as much as 145 kg N ha⁻¹ yr⁻¹. This large anthropogenic N input has the capacity to alter the composition of plant communities. We conducted N-fertilization experiments in chaparral and coastal sage scrub (CSS) stands over a five-year period to test the hypothesis that plant community composition would change in response to dry-season N addition because of an increase in the relative abundance of herbaceous plant species. Our results indicate that dry-season addition of N significantly altered the community composition of CSS but not chaparral. Contrary to our original hypothesis, changes in community composition were due to changes in the relative abundance of dominant shrubs and not herbaceous plant species. Given that community-level responses to changes in resource availability may take years to decades, in order to fully materialize, our results suggest that continued dry-season input of N will cause even larger changes in community composition over time. These results have implications for plant species composition and diversity of mediterranean-type shrublands as N deposition increases with population growth and fossil-fuel use.

Key words: Adenostoma fasciculatum; air pollution; Artemisia californica; Ceanothus greggii; disturbance; diversity; N-deposition treatments; plant community composition; Salvia mellifera; secondary succession; semiarid shrublands; southern California chaparral and coastal sage scrub.

INTRODUCTION

Atmospheric nitrogen (N) deposition from human activities has significantly increased since the beginning of the industrial revolution and is expected to increase with population growth (Fenn et al. 2003b, Galloway et al. 2004). Nitrogen deposition represents a significant input of N into many southern California (USA) semiarid ecosystems, where 85–95% of atmospheric N is in the form of dry deposition that is inputted to shrub and soil surfaces during the dry summer and fall months (Bytnerowicz and Fenn 1996, Fenn et al. 2003b, Tonnesen et al. 2007). Nitrogen deposition in heavily polluted southern California shrublands is estimated to be 20–45 kg N ha⁻¹ yr⁻¹ (Riggan et al. 1985, Bytnerowicz and Fenn 1996); however, more-exposed locales can receive up to 145 kg N ha⁻¹ yr⁻¹ (Fenn and Poth 2004).

Atmospheric N deposition has the capacity to alter plant community composition and diversity because of species differences in resource acquisition, resource-use efficiency, allocation, growth response, and competitive ability (Fenn et al. 2003a). In general, the abundance of fast-growing functional groups such as grasses and herbaceous annuals has been shown to increase significantly in response to N addition, often causing declines in plant species diversity (Goldberg and Miller 1990, Foster and Gross 1998, Zavaleta et al. 2003). However, changes in plant community composition may take several years because of the longer time scales associated with population- and community-level responses to changes in resource availability (Oechel and Vourlitis 1994, Milchunas and Lauenroth 1995). Furthermore, N-induced changes in plant species composition may interact with other agents of disturbance, such as fire and land-cover change (Lavorel et al. 1998, Minnich and Dezanni 1998, Fenn et al. 2003a), and environmental factors, such as rainfall and elevated CO₂ (Norby 1998), leading to complex population and community responses to atmospheric N deposition.

Chaparral and coastal sage scrub (CSS) shrublands represent >70% of the natural vegetation of the southern California coastal, interior, and mountain regions (Westman 1981) and are the main recipients of anthropogenic N. These shrublands are associated with large population centers (DiCastri 1991), high biodiversity (Cowling et al. 1996), and large numbers of endangered species (Dobson et al. 1997). Chaparral and CSS are relevant models for many semi-arid ecosystems worldwide, including Chilean matorral, Spanish maquis, South African fynbos and thorn-scrub, and Australian kwongan/mallee (DiCastri 1991), which share similar adaptations to drought, fire, and nutrient-poor soil (Cody and Mooney 1978, Bond and van Wilgen 1996). Thus,
mechanisms of how N deposition alters the community
dynamics of chaparral and CSS are applicable to
semi-arid shrublands worldwide.

Previous N-addition experiments (McMaster et al.
1982, Gray and Schlesinger 1983, Padgett and Allen
1999) have demonstrated significant increases in the
productivity of chaparral and CSS shrubs to added N;
however, these experiments have not addressed potential
community-scale effects of added N. Furthermore, these
experiments were conducted during the growing season
or in greenhouse environments where soil moisture was
ample and physiological activity was at a maximum, and
cannot address the potential for dry N inputs to alter the
relative abundance of plant species. Thus, to determine
the effects of dry N deposition on community composi-
tion we conducted a field N-fertilization experiment in
CSS and chaparral stands over a five-year period to
determine whether chronic, dry-season N inputs altered
the relative abundance of dominant and subdominant
shrubs and herbaceous plant species. Results from this
field experiment indicate that dry-season N addition
significantly increased N availability during the winter
and spring growing season (Vourlitis et al. 2007a) in part
because of higher rates of N mineralization (Vourlitis
and Zorba 2007, Vourlitis et al. 2007b, 2009). The
increase in N availability caused a significant increase in
the N concentration, and a reduction in the C:N ratio, of
aboveground tissue and litter; however, the production of
aboveground biomass and litter have not been signifi-
cantly affected by N addition at least during the first
five years of experimentation (Vourlitis et al. 2007a,
2009). Given the significant ecosystem N enrichment, we
hypothesized that plant community composition would
change in response to dry-season N addition because of
increases in the relative abundance of herbaceous plant
species.

Materials and Methods

Site descriptions

Field experiments have been conducted since Septem-
ber 2003 at the Santa Margarita Ecological Reserve
(SMER; 33°29′ N, 117°09′ W) and the Sky Oaks Field
Station (SOFS; 33°21′ N, 116°34′ W), California, USA.
Estimates of N-deposition exposure derived from a high-
resolution (4 km) model suggest both sites receive
approximately 6–8 kg N/ha annually (Tonnesen et al.
2007).

SMER is located in southwestern Riverside County,
California, USA, at an elevation of 338 m on a 9–11°
south–southwestern-facing slope. The site burned ∼35
years ago and is dominated by coastal sage scrub (CSS)
shrubs Artemisia californica Less. and Salvia mellifera
Greene that are summer deciduous (nomenclature
according to the Jepson Online Interchange for Cali-
ifornia Floristics).4 Soil is a sandy clay loam of the Las

4 [http://ucjeps.berkeley.edu/interchange.html]—

Posas Series derived of igneous and weathered Gabbro
material with a bulk density of 1.22 g/cm3 (Vourlitis et
al. 2007a). SMER receives an average of 36 cm of
rainfall annually, most of which occurs between
December and April.

SOFS is located in northeastern San Diego County,
California, USA, at an elevation of 1418 m on a 4–10°
southeast–southwest-facing slope. The stand burned in
July 2003, and unfortunately this unplanned perturba-
tion limits the potential for direct comparison to the
mature CSS stand. Before fire the site was a monocul-
ture of the evergreen shrub Adenostoma fasciculatum
H. & A., while after fire the stand was dominated by A.
fasciculatum with Ceanothus greggii A. Gray as a sub-
dominant. The site receives an average of 53 cm of pre-
cipitation annually, consisting of rain with occasional
snow that occurs primarily during the winter and spring.
The soil is an Ultic Haploxeroll derived of micaceous
schist with a sandy-loam texture and a bulk density of
1.34 g/cm3 (Vourlitis et al. 2007a).

Experimental design

The experimental layout at each site consisted of a
completely randomized design where four 10 × 10 m
plots received 50 kg N/ha as granular NH4NO3 (2003–
2006) or (NH4)2SO4 (2007–2008) and an additional four
10 × 10 m plots served as unmanipulated controls. Given
the estimated background levels of atmospheric N
deposition (6–8 kg N·ha⁻¹·yr⁻¹), plots exposed to added
N received 56–58 kg N·ha⁻¹·yr⁻¹ and control plots
received approximately 6–8 kg N·ha⁻¹·yr⁻¹. The added-
N treatment is generally higher than the level of N
deposition reported for urban chaparral shrublands (20–
45 kg N·ha⁻¹·yr⁻¹); however, the spatial pattern of N
deposition in southern California is highly variable and
poorly understood, and sites at slightly higher elevations
can receive between 40 and 145 kg N·ha⁻¹·yr⁻¹ (Fenn and
Poth 2004). This exposure level is also consistent with
that expected for southern Californian urban shrublands
over the next 2–3 decades (Fenn et al. 2003b, Galloway
et al. 2004). Beginning in September 2003, N fertilizer
was added as a single application in September of each year
using a handheld spreader, and while addition of
granular N may not be an adequate surrogate for
anthropogenic dry N deposition, our objective was not
to simulate dry N deposition per se but to determine if
dry-season N inputs altered the plant species composi-
tion of these mediterranean-type shrublands.

Aboveground biomass measurements

Aboveground biomass was measured every three
months from January 2004 to October 2008 (except
spring 2004) using nondestructive dimensional analysis
(Bonham 1989). Vegetation at least 20 cm in height was
measured within a 2-m-radius quadrat (12.57 m²) cen-
tered in each plot, while vegetation under 20 cm was
measured within a 0.5 × 0.5 m (0.25-m²) quadrat. Ve-
getation volume was calculated as the product of canopy
area \((A)\) and 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). Vegetation biomass was estimated from volume using regression equations that were developed for each species by harvesting measured plants of various sizes. Shrub dry mass and volume were ln-transformed to reduce variation, and coefficients-of-determination values \((r^2)\) for all regression equations were between 0.72 and 0.99 \((n = 42–26\) shrubs, depending on species). Generalized shrub and herbaceous-plant equations were used for species that did not occur frequently and/or regression equations were not made. The general herbaceous equation yielded an \(r^2\) of 0.79 \((n = 64\) shrubs), while the general shrub equation yielded an \(r^2\) of 0.97 \((n = 118\) shrubs). A bulk harvest of the 0.25-m² quadrat was used to determine herbaceous biomass in seasons when herbaceous plants were too numerous to be counted and measured individually.

**Data analysis**

For the chaparral stand, plant species were broken into four groups: (1) *A. fasciculatum*, (2) *C. greggii*, (3) other subdominant shrubs, such as *Trichostema parishii* Vasey and *Solanum xanti* A. Gray, and (4) herbaceous annuals, such as *Phacelia* spp. and *Cryptantha muricata* (Hook. & Arn.) A. Nelson & J. F. Macbr. For the CSS stand, plant species were also partitioned into four groups: (1) *A. californica*, (2) *S. mellifera*, (3) other subdominant shrubs, such as *Gutierrezia californica* (DC.) Toll. & A. Gray, and *Yucca whipplei* Toll., and (4) herbaceous annuals, such as *Gnaphalium* spp. The relative abundance of each species group was quantified as the proportion of the total biomass that was accounted for by each species group. Proportional biomass was used to quantify relative abundance since other, more traditional measures such as density and/or cover were not possible because herbaceous plants were at times too numerous to be individually counted and/or measured.

Percentage similarity in community composition between control and added-N plots was calculated using the Renkonen index (Krebs 1999):

\[
P_s = \frac{\sum \min(p_{Ci}, p_{Ni})}{\sum p_{Ci}}
\]

where \(P_s\) is the percentage similarity between control and added-N plots, \(p_{Ci}\) is the percentage of species group \(i\) in control plots, and \(p_{Ni}\) is the percentage of species group \(i\) in added-N plots. Temporal changes in \(P_s\) between added-N and control plots were assessed using linear regression with \(P_s\) as the dependent variable and time since January 2004 \((\text{months})\) as the independent variable. Repeated-measures ANOVA was used to assess whether N addition and time caused significant \((P < 0.05)\) variations in the relative composition of plant species and/or group. A significant direct effect of N addition and/or a significant N \(\times\) time interaction were taken to indicate a significant change in relative abundance in response to N addition. Box’s M and Mauchly’s tests (Weinfurt 2004) were used to test the assumptions of equality and compound symmetry (sphericity) of the between-group covariance matrices, respectively \((P <= 0.10)\), and corrected probability values were calculated using the Geisser-Greenhouse corrections for data that violated these assumptions (Hintze 2004). Statistical analyses were conducted using NCSS (version 2004; NCSS, Kaysville, Utah, USA).

**Results**

Percentage similarity \((P_s)\) in community composition of control and added-N plots declined significantly over the five-year field experiment in coastal sage scrub (CSS; Fig. 1a) due primarily to changes in the relative abundance of the dominant shrubs *Artemesia californica* and *Salvia mellifera* (Fig. 2a, b). For example, *A. californica* accounted for 60–80% of the total biomass in both control and added-N plots until the summer of 2006, but thereafter the relative abundance of *A. californica* in-

![Fig. 1. Changes in the percentage similarity in community composition, 2004–2008, between plots exposed to added and ambient N for (a) coastal sage scrub and (b) chaparral. Shown is the best-fit line, calculated from least-squares linear regression, between percentage similarity (dependent variable) and time since January 2004 (independent variable). Each panel includes the regression equation, coefficient of determination \((r^2)\), and probability \((P)\) that the slope of the line is significantly different from 0. Percentage similarity was calculated using Eq. 1. Seasons are: W = winter, Sp = spring, S = summer, F = fall.](image-url)
increased substantially in added-N plots leading to a significant $N \times$ time interaction (Fig. 2a). In contrast, *S. mellifera* accounted for 22–38% of the total biomass in control and added-N plots prior to fall 2005, but thereafter the relative abundance of *S. mellifera* was <40% in added-N plots and >40% in control plots, again resulting in a significant $N \times$ time interaction (Fig. 2b). The relative abundance of other subdominant shrubs or herbaceous plants was never very high in either control or added-N plots; however, other shrubs reached a peak of 16% in added-N plots in the summer and fall of 2006 (Fig. 2c) while herbaceous plants accounted for approximately 6–7% and 18–20% of the total biomass in the spring of 2005 and 2008, respectively (Fig. 2d).

In contrast, $P_a$ of control and added-N plots tended to increase over the five-year experiment in chaparral, but this trend was not statistically significant (Fig. 1b). On average added-N plots tended to have a lower relative abundance of *A. fasciculatum* (Fig. 3a) and a higher abundance of other shrub species (Fig. 3c) and herbaceous plants (Fig. 3c); however, these differences were not statistically significant. Regardless of N addition, *A. fasciculatum* accounted for most of the aboveground biomass, varying from a minimum of 40% in spring 2005 approximately two years post-fire to 85–95% in fall 2008 (Fig. 2a). The relative abundance of the other dominant shrub, *Ceanothus greggii*, reached a peak of ~30% in the summer of 2005 but declined to <10% by the end of 2008 (Fig. 3b). Other shrubs accounted for 10–15% of the total biomass in the summer of 2006, but their relative abundance was <10% for most of the five-year research period (Fig. 3c). Herbaceous biomass accounted for 30% (control) and 50% (added N) of the total biomass in 2005, but the contribution of herbaceous biomass declined over time regardless of N addition (Fig. 3d).

Species richness varied significantly over time for both CSS (Fig. 4a) and chaparral; however, there was no statistically significant effect of added N. Species richness in CSS varied between two and eight species and increased substantially in the spring of 2005, 2006, and 2008; however, there was no such increase in the spring of 2007 because of low rainfall. For chaparral, species richness tended to decline with time since fire, and while added-N plots had consistently higher species richness.
richness than control plots after summer 2005 this difference was not statistically significant (Fig. 4b). Seasonal increases in species richness were also apparent, and, as with CSS, species richness reached peaks in the spring of 2005, 2006, and 2008.

**DISCUSSION**

Our data support the hypothesis that plant community composition is altered by dry-season N addition in coastal sage scrub (CSS) but not chaparral over the five-year period observed here (Fig. 1), but, contrary to our original hypothesis, the change in community composition was not due to changes in the relative abundance of herbaceous plant species. Rather, floristic composition in CSS changed because plots exposed to added N became dominated by *Artemisia californica* at the expense of *Salvia mellifera* (Fig. 2). The increase in relative abundance of *A. californica* support results by Padgett and Allen (1999) who found that the biomass production of *A. californica* increased rapidly in response to N availability. The relative decline in *S. mellifera* suggests that added N significantly inhibited the biomass production and/or added N altered competitive dynamics between *A. californica* and *S. mellifera*. Unfortunately, neither mechanism can be ruled out with the data provided; however, added N also results in soil acidification (Vourlitis et al. 2007a, 2009), which may inhibit the growth and survival of shrubs (Roem et al. 2002).

The relative abundance of annual plants was not significantly affected by N addition at either of the study sites at least over the five-year research period. This is in contrast to recent results that suggest that dry N deposition can significantly increase the abundance of annual plants, especially nonnative grasses (Minnich and Dezzani 1998, Padgett and Allen 1999, Siguenza et al. 2006, Sirulnik et al. 2007a, b). At our CSS site, herbaceous species only accounted for 5–20% of the aboveground biomass depending on year and season (Fig. 2d), presumably because the dense shrub canopy limited the potential for annual-plant recruitment. In contrast, many of the CSS sites along the N-deposition gradient of the Riverside-Perris Plain, where the significant invasion of exotic annual grasses and forbs has been observed (Minnich and Dezzani 1998, Padgett and Allen 1999, Siguenza et al. 2006, Sirulnik et al.
long-term N addition may cause changes in species richness over time.

The relative abundance of the species and/or floristic groups exhibited significant temporal variations over the five-year study period regardless of N addition. For CSS and chaparral, there were significant increases in annual-plant abundance (Figs. 2d and 3d) and species richness (Fig. 4a, b) that coincided with seasonal variations in rainfall. The most obvious exception was in 2007 when annual-plant abundance and species richness varied little over the year. However, rainfall was 2–8 times lower in 2007 than in any other year, and annual-plant growth was undoubtedly limited by drought. In chaparral, herbaceous and other shrub species were relatively more abundant in chaparral plots during the 2004 and 2005 growing seasons, reflecting floristic changes during postfire succession (Moreno and Oechel 1991, Keeley 2000).

In conclusion, dry-season N addition was found to significantly alter the community composition of CSS shrublands over a five-year period. Changes in community composition were largely due to changes in the relative abundance of dominant shrubs and not herbaceous plant species as originally hypothesized. These data suggest that dry-season N inputs can substantially alter community composition over the short term, and given that community-level responses to resource perturbation may take years to decades to fully materialize (Oechel and Vourlitis 1994, Michunas and Lauenroth 1995), it is likely that continued inputs of N during the dry season will cause even larger changes in community composition over time. These results have implications for plant species diversity in mediterranean-type shrublands as N deposition increases with population growth and fossil-fuel use.

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