

High N, dry: Experimental nitrogen deposition exacerbates native shrub loss and nonnative plant invasion during extreme drought

Justin M. Valliere¹  | Irina C. Irvine² | Louis Santiago¹ | Edith B. Allen¹

¹Department of Botany and Plant Sciences and Center for Conservation Biology, University of California Riverside, Riverside, CA, USA

²Santa Monica Mountains National Recreation Area, U.S. National Park Service, Thousand Oaks, CA, USA

Correspondence

Justin M. Valliere, La Kretz Center for California Conservation Science, Institute of the Environment and Sustainability, University of California Los Angeles, Los Angeles, CA, USA.
Email: valliere@ucla.edu

Funding information

National Science Foundation, Grant/Award Number: DEB-1501110; National Park Service Air Resource Division, Grant/Award Number: J8C07110022

Abstract

Hotter, longer, and more frequent global change-type drought events may profoundly impact terrestrial ecosystems by triggering widespread vegetation mortality. However, severe drought is only one component of global change, and ecological effects of drought may be compounded by other drivers, such as anthropogenic nitrogen (N) deposition and nonnative plant invasion. Elevated N deposition, for example, may reduce drought tolerance through increased plant productivity, thereby contributing to drought-induced mortality. High N availability also often favors invasive, nonnative plant species, and the loss of woody vegetation due to drought may create a window of opportunity for these invaders. We investigated the effects of multiple levels of simulated N deposition on a Mediterranean-type shrubland plant community in southern California from 2011 to 2016, a period coinciding with an extreme, multiyear drought in the region. We hypothesized that N addition would increase native shrub productivity, but that this would increase susceptibility to drought and result in increased shrub loss over time. We also predicted that N addition would favor nonnatives, especially annual grasses, leading to higher biomass and cover of these species. Consistent with these hypotheses, we found that high N availability increased native shrub canopy loss and mortality, likely due to the higher productivity and leaf area and reduced water-use efficiency we observed in shrubs subject to N addition. As native shrub cover declined, we also observed a concomitant increase in cover and biomass of nonnative annuals, particularly under high levels of experimental N deposition. Together, these results suggest that the impacts of extended drought on shrubland ecosystems may be more severe under elevated N deposition, potentially contributing to the widespread loss of native woody species and vegetation-type conversion.

KEYWORDS

coastal sage scrub, drought, Mediterranean-type shrublands, nitrogen deposition, nonnative plant invasion, shrub loss, vegetation-type conversion

1 | INTRODUCTION

Episodes of intense, prolonged drought are predicted to increase worldwide with future changes in climate (Bell, Sloan, & Snyder,

2004; Dai, 2013). Hotter, longer, and more frequent global change-type drought events may profoundly alter ecosystem structure, function, and services by triggering widespread vegetation die-off (Anderegg, Kane, & Anderegg, 2013; Breshears et al., 2005). Indeed,

drought associated with climate change has already been identified as responsible for large-scale mortality of woody vegetation across continents (Adams et al., 2009; Allen, Macalady et al., 2010; Peñuelas, Lloret, & Montoya, 2001). Such drought-induced loss of woody vegetation may cause dramatic shifts in plant species and, in the most extreme scenario, result in complete vegetation-type conversion (Allen & Breshears, 1998; Mueller et al., 2005). However, extreme climate events are not the sole driver of environmental change, and the ecological impacts of drought may be compounded by other components of global environmental change such as nitrogen (N) deposition (Bobbink et al., 2010; De Marco et al., 2014; Friedrich et al., 2012) and nonnative plant invasion (Dale et al., 2001; Manea, Sloane, & Leishman, 2016).

Atmospheric pollution from anthropogenic activities contains substantial amounts of reactive N that is ultimately deposited to the earth's surface, and global N inputs have risen dramatically with increased industry and agriculture (Galloway, 2005; Vitousek et al., 1997). Soil N enrichment due to N deposition may negatively impact native plant communities by reducing plant diversity (Bobbink et al., 2010; Simkin et al., 2016) and facilitating nonnative plant invasion (Davis, Grime, & Thompson, 2000; Dukes & Mooney, 1999). In some instances, this results in complete vegetation-type conversion, such as the conversion of native coastal sage scrub (CSS) shrublands to invasive-dominated annual grasslands in southern California, USA (Allen, Egerton-Warburton, Hilbig, & Valliere, 2016; Cox, Preston, Johnson, Minnich, & Allen, 2014; Talluto & Suding, 2008).

Southern California experiences some of the highest levels of N deposition in the United States, with levels ranging from 20 to 45 kg ha⁻¹ year⁻¹ or greater in urban areas (Fenn et al., 2003). As in other arid and semiarid ecosystems, this falls largely as dry deposition during the summer dry period, entering the system as a sudden pulse of N with the first rains of the winter growing season (Allen, Padgett, Bytnerowicz, & Minnich, 1998; Padgett, Allen, Bytnerowicz, & Minich, 1999). The resulting increase in soil N appears to favor nonnative species, particularly annual grasses, over natives (Allen et al., 1998; Kimball, Goulden, Suding, & Parker, 2014; Wood, Meixner, Shouse, & Allen, 2006), although this has not been observed in all cases (Vourlitis & Pasquini, 2009). Along with other Mediterranean ecosystems worldwide, such as the Chilean matorral, Spanish maquis, South African fynbos, and Australian kwongan, California's Mediterranean vegetation has been identified as a biodiversity "hot-spot," constituting a major conservation priority (Mittermeier, Myers, Mittermeier, & Robles Gil, 1999; Myers, Mittermeier, Mittermeier, Da Fonseca, & Kent, 2000). These Mediterranean ecoregions may be particularly vulnerable to changes in climate (Loarie et al., 2008; Midgley, Hannah, Millar, Rutherford, & Powrie, 2002) and elevated N deposition (Phoenix et al., 2006; Sala et al., 2000), but interactions between these global change drivers are not well understood.

Individually, both N deposition and drought may favor conversion of shrublands to nonnative annual grasslands (Cox et al., 2014; Kimball et al., 2014; Minnich & Dezzani, 1998), and these factors may also have interactive effects. For example, while native woody species may exhibit positive growth responses under elevated N

availability (Padgett & Allen, 1999), this could also increase susceptibility to drought (Valliere & Allen, 2016a). Work in other ecosystems has found that higher plant productivity due to N deposition may decrease drought tolerance, resulting in increased mortality (Bobbink & Lamers, 2002; Friedrich et al., 2012; Meyer-Grünefeldt, Friedrich, Klotz, Von Oheimb, & Härdtle, 2015), but direct evidence from field studies is severely lacking. In one study, Kimball et al. (2014) found reduced water inputs in conjunction with N fertilization retarded postfire recovery of CSS shrublands, but it is unclear how these two factors will influence mature vegetation.

Plant functional traits may help explain community response to N deposition and drought. For example, Pivovarovoff, Santiago, Vourlitis, Grantz, and Allen (2016) explored hydraulic responses of native woody CSS species to long-term N fertilization, finding N addition may alter drought tolerance in some species; however, it remains to be determined whether these trait responses will impact community-level dynamics. Jones Paine, Fenn, and Poth (2004), working in ponderosa and Jeffrey pine forests of southern California, reported higher tree mortality at high N deposition sites in response to drought and bark beetle activity, while Allen, Allen et al. (2010) observed similar increased mortality of N-fertilized pinyon pines due to decreased plant water-use efficiency (WUE). Collectively, these studies suggest a strong potential for N deposition to alter plant traits and exacerbate drought-induced vegetation mortality in Mediterranean-type shrublands such as CSS.

Since 2011 and as of this writing, California has experienced an exceptionally severe drought driven by below-average precipitation combined with record high temperatures (Fahrenkamp-Uppenbrink, 2015; Griffin & Anchukaitis, 2014). This has resulted in widespread increases in plant water stress at the landscape level (Asner et al., 2016) and dieback of woody vegetation, including CSS (Coates, Denison, Roberts, & Roth, 2015). As in other Mediterranean regions, rainfall in southern California is highly variable from year to year, as well as within years (Haston & Michaelsen, 1997). Some woody perennials from Mediterranean ecoregions are adapted to withstand short-term seasonal drought through avoidance; multiple shrub species are drought deciduous. However, prolonged drought may result in canopy dieback and mortality due to hydraulic failure, depletion of carbohydrate reserves, or increased susceptibility to herbivory and other stressors (McDowell et al., 2008). Drought has been cited as a possible cause of conversion of CSS to nonnative-dominated annual grasslands (Kimball et al., 2014; Minnich & Dezzani, 1998), and N deposition could intensify this effect by contributing to higher mortality of woody species while simultaneously increasing growth of nonnative annuals.

Here, we present the results of a five-year field study in which we tested the response of a Mediterranean-type shrubland plant community in southern California to multiple levels of N addition during an extreme, multiyear drought. While drought was not an explicit component of our original experimental design, the initiation of the study coincided with the onset of the Great California Drought in 2011 (Fahrenkamp-Uppenbrink, 2015; Griffin & Anchukaitis, 2014), raising the question how does N availability influence

the persistence of woody vegetation and community composition during protracted drought? Specifically, we asked the following: (1) How does simulated N deposition influence native shrub canopy cover and mortality during a multiyear drought? (2) Are there changes in plant functional traits due to N addition that alter the response of native shrubs to drought? (3) In the event of drought-induced shrub loss, does N addition increase invasion of nonnative plant species? We hypothesized that native shrub cover would decline over time due to drought-induced shrub mortality and canopy dieback, especially under high N addition. We also predicted that native shrub loss would be accompanied by changes in plant functional traits, such as productivity, leaf area, and WUE. For example, increased leaf area and productivity under high N could increase plant water demand and decrease plant WUE.

As human activities continue to contribute to elevated atmospheric N inputs (Galloway, 2005; Vitousek et al., 1997), changes in climate (Bell et al., 2004; Loarie et al., 2008), and the global homogenization of species (Hobbs, 2000), understanding the ecological consequences of these factors in concert will be increasingly important. Our results have important implications for the persistence and conservation of Mediterranean-type ecosystems under future global change.

2 | MATERIALS AND METHODS

2.1 | Study site

We conducted our field experiment at Rancho Sierra Vista (34.15° N, 118.96° W), a unit of the Santa Monica Mountains National Recreation Area in southern California, USA. The region experiences a typical Mediterranean-type climate, with hot dry

summers, and variable precipitation occurring during the cooler winter–spring months. Mean annual precipitation at the site is 420 mm; however, rainfall has been below average since the study was initiated in 2011 (Figure 1a). Modeled rates of N deposition for the site are approximately 8 kg N ha⁻¹ year⁻¹ (Fenn et al., 2010; Tonnesen, Wang, Omary, & Vhien, 2007), but deposition rates based on atmospheric N concentrations are much lower at <3 kg N ha⁻¹ year⁻¹ (Valliere, 2016). The site last burned in 1993. Soils at the site are loamy, shallow Entic Haploxerolls in the Cotharin series.

2.2 | Precipitation data

We obtained daily precipitation data for the study site from the PRISM Climate Group at Oregon State University, USA (<http://prism.oregonstate.edu>, October 2016). Data are based on a 4 km grid interpolation using source data from multiple stations (Daly et al., 2008). From these data, we calculated annual and monthly rainfall totals during the study period as well as 30-year averages (Figure 1a).

2.3 | Nitrogen addition plots

We installed experimental N addition plots in November 2011, prior to the first rains of the winter–spring growing season. Plots measured 6 × 6 m and were located in mature CSS dominated by *Artemisia californica* Less. (Asteraceae), a drought-deciduous shrub that is the foundation species of CSS. Plots were fertilized annually in the fall, simulating the accumulation of dry N deposition during summer months, at one of four rates of N addition from calcium nitrate (CaN₂O₆) and urea (CH₄N₂O): control (C) = 0 g N/m²; low (L) = 0.5 g N/m²; medium (M) = 1.5 g N/m²; high (H) = 3 g N/m². The

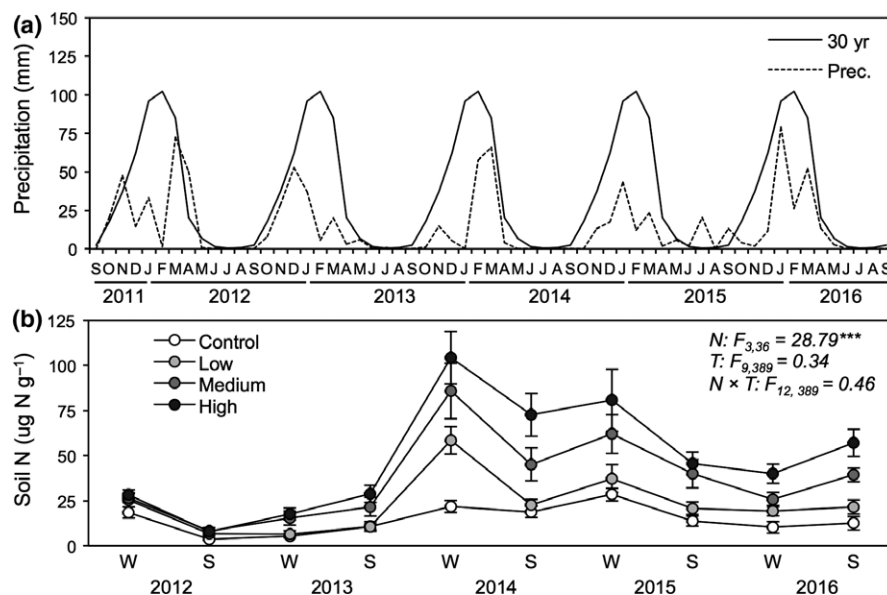


FIGURE 1 Monthly total precipitation from September 2011 to September 2016 (dashed line) and monthly 30-year (1981–2010) rainfall averages (solid line) for the study site (a). Data retrieved from Oregon State's PRISM Climate Group <http://www.prism.oregonstate.edu/>, created October 30, 2016. Mean total extractable N of soils (b) from N addition plots (control = 0 g N/m²; low = 0.5 g N/m²; medium = 1.5 g N/m²; high = 3.0 g N/m²) over time, from winter (W) 2012 to summer (S) 2016. Values represent means ± SE. Also shown are F statistics and significance levels from repeated-measures ANOVA for nitrogen (N), time (T), and their interaction (N × T). *p < .05, **p < .001, ***p < .0001

two forms of N were mixed prior to application and spread by hand. These rates of N addition correspond to the ranges of N deposition in the region (Fenn et al., 2010; Tonnesen et al., 2007). We included ten replicate plots at each N addition level and controls in a randomized block design, for a total of 10 blocks and 40 plots.

2.4 | Soil nitrogen and other characteristics

Between 2011 and 2016, we collected soils for extractable N analysis seasonally, sampling during the winter growing season and again during the summer dry period once vegetation had senesced, usually in March and September, respectively. Within each plot, we took three 2.5 × 10 cm deep soil cores at each sampling period that were composited (by plot) for analysis. Soil N was extracted using potassium chloride (KCl) and analyzed using an AQ2 Discrete Analyzer (SEAL Analytical, Inc., Southampton, UK) at the University of California, Riverside. Soil pH was measured on samples taken seasonally with a pH meter in a 1:1 soil:water slurry. Soil samples taken the first year of the study were analyzed at the University of California, Davis, Analytical Laboratory for soil nutrients including phosphorus (Olsen-P) and exchangeable cations and soil texture (Table 1).

2.5 | Vegetation sampling

Vegetation sampling was conducted in the interior 5 × 5 m of plots to limit edge effects. We measured shrub cover along three permanent, evenly spaced 5 m transects per plot each year in the spring from 2012 to 2016 at the peak of the growing season, April to May. Along transects, we measured the total distance in cm of each plant that intercepted the line by species. Shrub mortality was assessed by counting the number of live and dead shrubs within plots. We also collected fresh leaf tissue for determination of leaf N and C content and C isotopic composition from *A. californica* shrubs within each

TABLE 1 Soil characteristics at the research site including available phosphorus (Olsen-P), concentrations of exchangeable cations (K = potassium, Na = sodium, Ca = calcium, Mg = magnesium), total percent C and N, and soil texture (percent composition of sand, silt, and clay). Values are means ± SE

Parameter	Unit	Average
<i>Soil nutrients</i>		
P	ppm	18.8 ± 2.9
K	ppm	305.2 ± 55.9
Na	ppm	44.8 ± 1.6
Ca	meq/100 g	11.6 ± 1.8
Mg	meq/100 g	5.2 ± 0.5
Total C	%	0.51 ± 0.05
Total N	%	0.05 ± 0.01
<i>Soil texture</i>		
Sand (%)	%	64.1 ± 5.0
Silt (%)	%	23.2 ± 1.9
Clay (%)	%	13.8 ± 0.5

plot. We sampled cover of herbaceous/annual vegetation by species each spring using four replicate 1 × 0.5 m gridded quadrats per plot. In a subset of quadrats, herbaceous vegetation was clipped to determine plant biomass. Herbaceous biomass was then estimated using regression equations from ln-transformed cover and dry mass data. Finally, each year, we recorded total species richness within plots.

2.6 | Leaf traits

Each spring, we collected terminal shoots representing the new season's growth from mature *A. californica* shrubs for measurement of leaf-level traits including leaf area (LA), specific leaf area (SLA), and leaf:sapwood area ratio (LA:SA). We collected three replicate terminal shoots cut directly above the terminal bud scale scar (marking the previous year's growth) from one shrub per plot. Samples were placed in plastic bags with wet paper towels and transported to the laboratory where leaf area was measured using a LI-3100C Area Meter (LI-COR, Inc., Lincoln, NE USA) within 24 hr of collection. Sapwood area was estimated by taking the diameter of the stem and converting this value to the area of a circle. Leaf tissue from *A. californica* shrubs was dried for 48 hr at 60°C, ground, and analyzed for percent C and N using a Thermo-Finnigan FlashEA 1112 Nitrogen and Carbon Analyzer (Thermo Fisher Scientific, Waltham, MA, USA) at the University of California, Riverside, Environmental Science Research Laboratory.

2.7 | Leaf $\delta^{13}\text{C}$

We analyzed leaf tissue samples from *A. californica* shrubs in control and high N addition plots for carbon stable isotope ratios ($\delta^{13}\text{C}$) for the assessment of intrinsic WUE (Farquhar, Ehleringer, & Hubick, 1989). Isotopic analysis was conducted at the University of California, Riverside, Facility for Isotope Ratio Mass Spectrometry using an elemental analyzer (ECS 4010; Costech, Valencia, CA, USA).

2.8 | Productivity

To measure potential changes in litter production and shrub productivity, at the end of the 2012 growing season, we installed litter traps below mature *A. californica* shrubs in plots receiving three levels of N addition (0, 1.5, and 3 g N/m²). Litter traps consisted of a 20 × 25 cm rectangular wooden frame with a stainless steel mesh bottom. Litter samples were collected regularly until summer 2016 (every 1–4 months depending on litter-fall), dried at 60°C, sorted into leaf and woody litter, and weighed.

2.9 | Data analysis

We used repeated-measures analysis of variance (ANOVA), where year was the repeated measure, to assess whether N addition caused significant variation in soil N, leaf tissue N, leaf tissue $\delta^{13}\text{C}$, shrub biomass, cover and productivity, native and nonnative herbaceous cover and biomass, and species richness. We interpreted a significant ($p < .05$) direct effect of N treatment or N × time interaction

as evidence that N addition had resulted in significant changes to the plant community. Prior to analysis, we tested data for variance–covariance homogeneity and sphericity using Box's *M* and Mauchly's tests, respectively. Data that violated these assumptions were analyzed using Geisser–Greenhouse corrections. Leaf-level traits were analyzed within year using ANOVA. We also used one-way ANOVA to test the effects of N addition on plant and community response variables within years. Statistical analyses were conducted using SAS (version 2013; SAS Institute Inc., Cary, NC, USA).

3 | RESULTS

3.1 | Precipitation

Precipitation was below average for the duration of the study (Welch–Satterthwaite two-sample *t* test; $t_{1,223} = 3.56$, $p = .0004$; Figure 1a). Monthly rainfall totals were below 30-year averages 56 of the 61 months during the study period.

3.2 | Soil nitrogen

Following an initial lag period, N addition enhanced soil N availability over time (Figure 1b), with N availability incrementally higher in each of the N addition treatments. This pattern persisted for the duration of the study, with some seasonal variation. Soil pH varied with time ($F_{12,389} = 34.94$, $p = .0004$), but no changes in soil pH due to N ($F_{3,36} = 1.03$, $p = .2345$) or N by time interaction ($F_{12,389} = 1.15$, $p = .0950$) were detected. Mean soil pH across N treatments and years was 6.5 ± 0.04 .

3.3 | Shrub cover

Native shrub cover, consisting primarily of the shrub *A. californica*, was dramatically reduced over time in all treatments (Figure 2a; Table S1), from a baseline average of 70% cover to an eventual average of ~30% cover in control plots. Other shrub species included

Acmispon glaber (Vogel) Brouillet and *Baccharis pilularis* DC., which combined formed 6% of shrub cover in 2012 and 5% in 2016. Shrub loss was particularly pronounced in the high and medium N addition treatments, in which we observed the lowest shrub cover in the final years of the study at 16% and 20%, respectively (Figure 2a). Loss of the shrub canopy was due to both dieback of branches (as evidenced by litter trap data shown below) and shrub mortality. After 5 years, an average of 38% of *A. californica* shrubs died in control plots (Figure 2b). Addition of N also increased shrub mortality, with the highest percentage of shrub die-off observed in the high N treatment at an average of 54% mortality (Figure 2b).

3.4 | Shrub productivity

The production of leaf and woody litter varied over time and with N addition (Figure 3a,b). In the first year of the study, leaf litter production was 40% higher for shrubs within high N plots relative to controls (Figure 3a). However, following a steep drop in 2014 across all treatments, leaf litter production recovered in control but not high N addition plots, and by the close of the study, leaf litter production of shrubs in control plots was more than double that of those receiving the highest level of N addition (Figure 3a). Experimental N deposition also influenced woody litter drop, with higher woody litter production observed in high N plots in three of the 4 years for which data were collected (Figure 3b).

3.5 | Leaf traits

Elevated N availability resulted in increases in leaf area of terminal shoots of *A. californica* shrubs in all years measured, but only in plots receiving the highest amount of N fertilization (Table 2). While leaf area increased with N addition, we observed no significant changes in SLA across N treatments (Table 2). In 2 years, 2015 and 2016, shrubs within medium and high N addition plots exhibited higher LA:SA (Table 2). We also detected significant effects of simulated N deposition on C and N content of *A. californica* leaves, with N

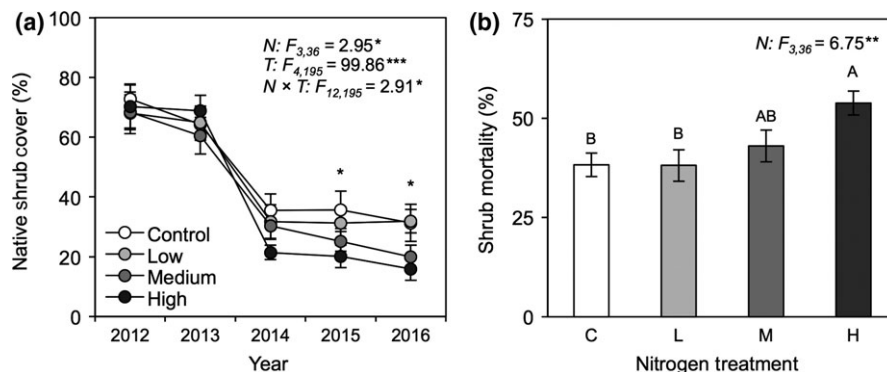


FIGURE 2 Native shrub cover through time from 2012 to 2016 (a) and cumulative percent shrub mortality at the end of the study period (b) within N addition plots (control = 0 g N/m²; low = 0.5 g N/m²; medium = 1.5 g N/m²; high = 3.0 g N/m²) and *F* statistics and significance levels from repeated-measures ANOVA. Values represent means \pm SE. * $p < .05$, ** $p < .001$, *** $p < .0001$. Asterisks above yearly shrub cover data represent significant effects ($p < .05$) of N within years from ANOVA. Different letters above bars representing percent shrub mortality indicate values were significantly different (ANOVA; Tukey's HSD)

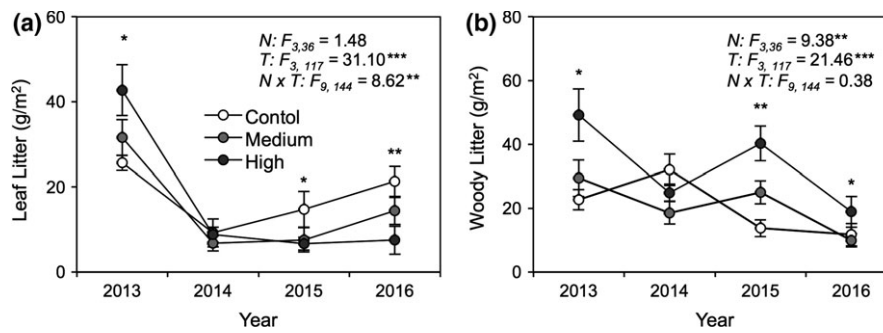


FIGURE 3 Mean leaf litter (a) and woody litter (b) biomass production per m² of *Artemisia californica* shrubs from litter traps within N addition plots (control = 0 g N/m²; medium = 1.5 g N/m²; high = 3.0 g N/m²) through time from 2013 to 2016 and F statistics and significance levels from repeated-measures ANOVA for nitrogen (N), time (T), and their interaction (N × T). Values represent means ± SE. Asterisks above data points indicate significant effect of N when analyzed with ANOVA by year. * $p < .05$, ** $p < .001$, *** $p < .0001$

TABLE 2 Leaf-level traits of *Artemisia californica* including mean leaf area (LA), specific leaf area (SLA), and the ratio of leaf area to sapwood area (LA:SA) from terminal branches representing new growth collected each spring from 2013 to 2016 from N addition plots (C = 0 g N/m²; L = 0.5 g N/m²; M = 1.5 g N/m²; H = 3.0 g N/m²). Values in the same row, for each year, followed by different letters are significantly different based on ANOVA

Year	LA						SLA						LA:SA					
	N Treatment				F	p	N Treatment				F	p	N Treatment				F	p
C	L	M	H	C			L	M	H	C			L	M	H			
2013	11.6b	14.5ab	16.1b	16.3b	2.92	.0478	129.7	135.5	134.9	133.8	0.14	.9337	2.2	2.3	2.5	2.6	1.32	.2831
2014	8.2b	8.3b	13.9a	15.8a	11.36	<.0001	132.5	128.8	134.7	128.2	0.23	.8745	2.3	2.3	2.2	2.6	0.48	.6976
2015	9.1b	11.9ab	11.5ab	15.0a	2.93	.0471	132.5	128.8	134.7	128.2	0.06	.9783	2.1b	2.7ab	2.4ab	3.0a	2.89	.0409
2016	9.6b	12.0ab	11.7ab	13.6a	3.26	.0263	129.3	131.1	131.6	131.2	0.08	.9732	2.7b	3.2ab	3.1ab	3.6a	2.93	.0394

Bold values represent a significant statistical difference was detected.

addition leading to higher percent N, and reduced C:N ratios in four of the five years measured (Table 3). In 2014 and 2015, this increase in N content was also accompanied by a significant reduction in percent leaf C (Table 3).

3.6 | Leaf $\delta^{13}\text{C}$

Carbon stable isotope ratio of leaf tissue from *A. californica* shrubs was altered by the addition of N, with shrubs from control plots exhibiting higher (less negative) $\delta^{13}\text{C}$ values in multiple years compared to shrubs from high N addition plots (Figure 4). The lower (more negative) $\delta^{13}\text{C}$ of leaves from high N shrubs indicates reduced intrinsic WUE relative to control plots (Farquhar et al., 1989).

3.7 | Herbaceous vegetation

We also observed changes in cover and biomass of herbaceous plant species over five years of drought, with significant effects of N addition also detected (Figure 5a–f). The cover of native herbaceous species varied by year, ranging from <2% cover on average in 2012, to an average of ~20% in 2015 and 2016 within control plots (Figure 5a; Table S1). Experimental N reduced the cover of these species at every level of N addition in 2016 compared to control plots. The cover of nonnative species was generally higher than native herbaceous cover and increased over time, save for a drop in

cover across all treatments in 2014 (Figure 5b; Table S1). Nitrogen had a positive effect on total nonnative cover (Figure 5b), including nonnative annual grasses (Figure 5c) and forbs (Figure 5d). However, nonnative annual grass cover was higher than that of nonnative forbs, and these groups of plants responded differently over time; annual grass cover showed a positive response to N addition in 2013 and 2016, and annual forbs in 2013 and 2015. Biomass per m² of native and nonnative herbaceous plant species generally increased over the 5 years of the study in control plots, with nonnative biomass higher than that of native herbaceous species at every sampling period (Figure 5e,f). Native herbaceous biomass was impacted by N addition, but this response differed by year; in 2015, the highest level of N addition resulted in increased native biomass, while in 2016, native biomass was reduced by approximately 30% with any level of N addition relative to control plots (Figure 5e).

Nonnative biomass showed a strong positive response to N addition in all years except the first, and in the final years of the study, biomass of nonnatives was two to three times higher in plots receiving medium and high rates of simulated N deposition compared to control plots (Figure 5f).

3.8 | Species richness

Mean native species richness within plots increased over time (Time, $F_{4,195} = 183.11$, $p < .0001$), with the highest number of native

TABLE 3 Mean foliar percent N, percent C, and C:N ratio of *Artemisia californica* shrubs within N addition plots (C = 0 g N/m²; L = 0.5 g N/m²; M = 1.5 g N/m²; H = 3.0 g N/m²) from spring 2012 to spring 2016. Values for each parameter with different letters within the same row are significantly different based on ANOVA

Year	Leaf tissue N (%)						Leaf tissue C (%)						Leaf tissue C:N						
	N Treatment			F			N Treatment			F			N Treatment			F			
	C	L	M	H	M	H	C	L	M	H	M	H	C	L	M	H	M	H	F
2012	2.16b	2.14b	2.44a	2.40a	6.79	.0010	47.26	46.55	47.91	47.01	47.01	0.59	.6271	20.02a	21.90a	19.73b	19.69b	7.01	.0008
2013	2.36	2.64	2.37	2.58	2.09	.1182	47.64	47.88	47.74	47.57	47.57	0.53	.6651	20.51	20.23	18.51	18.62	2.16	.1092
2014	2.92ab	2.64b	2.85a	3.22a	4.90	.0059	47.18a	46.89ab	46.88ab	46.11b	46.11b	3.03	.0420	16.60a	17.87a	16.42a	14.41b	6.27	.0015
2015	2.90b	2.98b	3.54a	3.67a	10.11	<.0001	47.85a	47.85a	48.34a	46.84b	46.84b	14.39	<.0001	16.33a	16.15a	13.97b	13.12b	9.27	<.0001
2016	2.79b	2.88b	2.88b	3.41a	5.03	.0131	46.93	47.34	47.24	47.20	47.20	0.71	.5518	17.16a	16.60ab	16.58ab	14.08b	3.51	.0418

Bold values represent a significant statistical difference was detected.

species observed in 2015 (Table 4). This was due to higher occurrences of annual and herbaceous perennial species within plots over time. There was no effect of N addition (N, $F_{3,36} = 0.53$, $p = .6620$; N \times time $F_{12,195} = 0.58$, $p = .6620$) on native plant richness (Table 4). Nonnative species richness was generally lower than native richness, but showed a similar pattern of increasing over time (time, $F_{4,195} = 96.27$, $p < .0001$; Table 4). There was no effect of N addition on nonnative richness when data were analyzed across all years (N, $F_{3,36} = 2.48$, $p = .6420$; N \times time $F_{12,195} = 0.72$, $p = .5437$). However, when we analyzed data within years (ANOVA), in both 2013 and 2015, plots receiving the highest level of N addition had more nonnative species on average than control plots (Table 4).

In addition to *A. californica* and other shrubs, native herbaceous species included *Chenopodium californicum* S. Watson, *Crassula conata* Ruiz & Pav., *Cryptantha intermedia* (A. Gray) Greene, *Dichelostemma capitatum* Wood, and *Euphorbia albomarginata* A. Gray. Dominant nonnative species were *Bromus rubens* L., *Centaurea melitensis* L., *Erodium cicutarium* L., *Hirschfeldia incana* L., and *Schismus arabicus* Nees.

4 | DISCUSSION

Our results demonstrate simulated N deposition likely contributed to native CSS shrub canopy dieback and mortality and concomitant increases in nonnative annual plant species during an extreme, multi-year drought event in southern California. The observed loss of native shrub cover was accompanied by changes in plant functional traits of the dominant shrub species, *A. californica*, in response to N addition, including increased leaf litter production (initially), leaf area, LA:SA, and leaf percent N, and decreased WUE. This work supports the hypothesis that N deposition may increase the severity of the negative ecological consequences of other global change drivers, such as changes in climate and nonnative plant invasion (Bobbink et al., 2010; Dukes & Mooney, 1999).

Addition of N dramatically increased soil N availability over time, with levels as high as 100 N $\mu\text{g/g}$ in plots receiving 3 g N m^{-2} year⁻¹, five times those typical of sites receiving ambient levels of N deposition (Fenn et al., 2010; Padgett et al., 1999). As in other seasonally dry ecosystems, N inputs resulting from atmospheric pollution typically accumulate on soil and plant surfaces as dry deposition during the summer dry period, later becoming available for uptake with the first winter rains. Thus, soil N availability at high-deposition sites peaks with the first rains of the growing season, after which N decreases to levels comparable with low-deposition sites as N is immobilized by plant uptake and leached from the soil (Fenn et al., 2003; Padgett et al., 1999). However, our results show that during extended periods of low rainfall, N continues to accumulate and remains in the soil over years. This suggests that during prolonged drought, even relatively low chronic N inputs could result in significantly elevated soil N availability.

The accumulation of soil N that we observed with N addition is likely due to reduced plant activity, uptake and leaching during

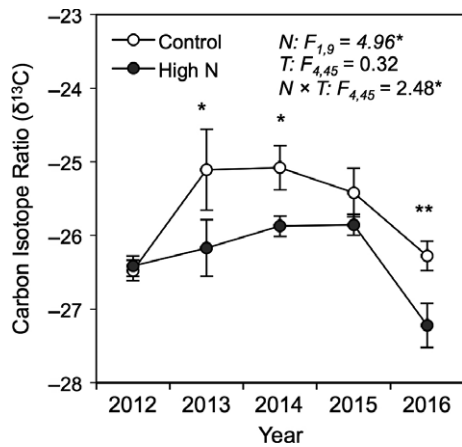


FIGURE 4 Carbon isotope ratio ($\delta^{13}\text{C}$) of leaf tissue from *Artemisia californica* shrubs within control plots (control) and plots receiving $3 \text{ g N m}^{-2} \text{ year}^{-1}$ (high N) over time from 2012 to 2016. Values represent means \pm SE. Also shown are F statistics and significance levels from repeated-measures ANOVA for nitrogen (N), time (T), and their interaction (N \times T). Asterisks above data points indicate a significant effect of N addition within years from one-way ANOVA. * $p < .05$, ** $p < .001$, *** $p < .0001$

prolonged drought conditions. We also observed higher foliar N concentrations in native shrubs and increased litter-fall in N addition plots, which could have contributed to soil N pools. Others have found increased rates of N mineralization with N addition (Sirulnik, Allen, Meixner, & Allen, 2007; Voullitis, Zorba, Pasquini, & Mustard, 2007), and this may have had an effect in our soils. Nonnative species can also strongly influence soil nutrient cycling (Ehrenfeld, 2003), and there is evidence that nonnative annual grasses may increase pools of N and rates of mineralization and nitrification (Hawkes, Wren, Herman, & Firestone, 2005; Parker & Schimel, 2010). Thus, higher nonnative cover and biomass in N addition plots could have also contributed to observed levels of N availability.

Over 5 years of below-average rainfall and record high temperatures, native shrub cover was greatly reduced due to dieback of branches and entire shrubs. This is consistent with previous reports of CSS shrub mortality during extended drought (Minnich & Dezzani, 1998) and recent documentation of vegetation dieback in southern California during the same study period using hyperspectral and infrared aerial imagery (Coates et al., 2015). Similar widespread drought-induced shrub loss was previously documented in Spanish shrublands (Peñuelas et al., 2001). We found native shrub loss was

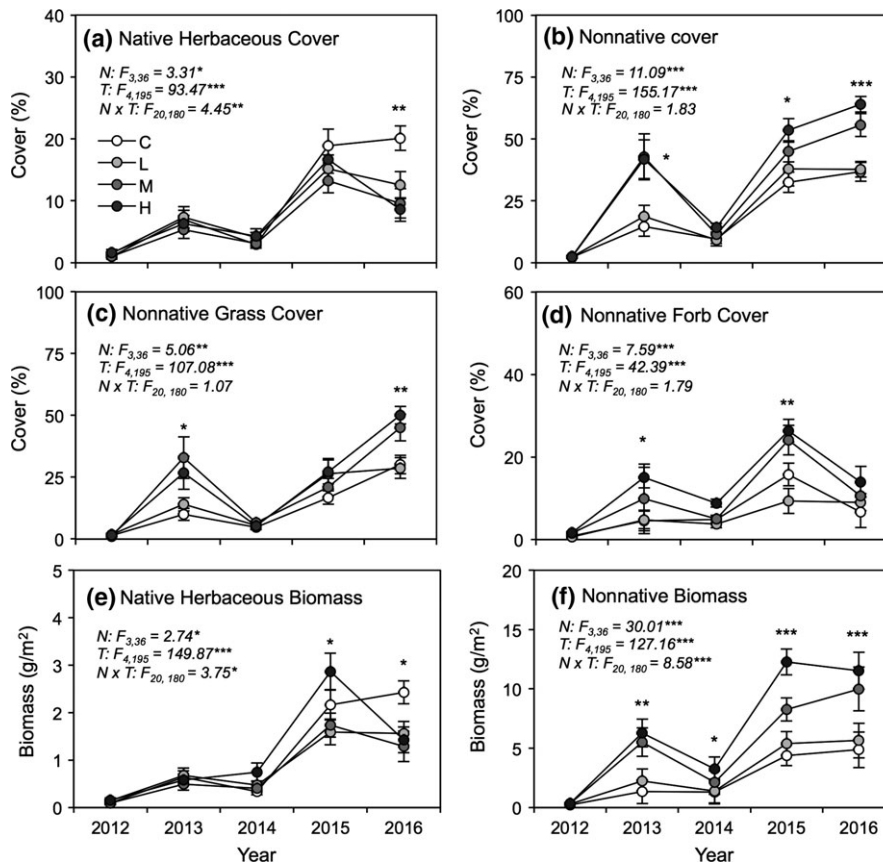


FIGURE 5 Total native herbaceous cover (a), total nonnative cover (b), nonnative forb cover (c), nonnative annual grass cover (d), native herbaceous biomass (e), and nonnative biomass (f) within N addition plots (C = 0 g N/m^2 ; L = 0.5 g N/m^2 ; M = 1.5 g N/m^2 ; H = 3.0 g N/m^2) through time from 2012 to 2016. Also shown are F statistics and significance levels from repeated measures ANOVA for nitrogen (N), time (T) and their interaction (N \times T). Asterisks above data points indicate a significant effect of N addition within years from one-way ANOVA. Values represent means \pm SE. Note different y-axis labels and scale. * $p < .05$, ** $p < .001$, *** $p < .0001$

TABLE 4 Mean native plant richness, invasive plant richness, and total plant richness within experimental N addition plots (C = 0 g N/m²; L = 0.5 g N/m²; M = 1.5 g N/m²; H = 3.0 g N/m²) from spring 2012 to spring 2016 and ANOVA statistics. Values in the same row for each year followed by different letters are significantly different ($p < .05$)

Year	Native Richness						Nonnative Richness						Total Richness					
	N Treatment						N Treatment						N Treatment					
	C	L	M	H	F	p	C	L	M	H	F	p	C	L	M	H	F	p
2012	3.1	3.6	3.1	3.6	1.63	.2034	3.5	3.3	3.4	3.3	0.80	.9681	6.6	6.9	6.5	6.9	0.31	.8239
2013	4.6	4.5	4.0	4.2	0.38	.7704	3.8b	4.3ab	4.8ab	5.4a	4.48	.0090	8.4	8.8	8.8	9.6	0.61	.6141
2014	5.0	5.3	5.9	5.1	0.51	.6756	4.6	4.6	5.2	5.3	0.88	.4821	9.6	10.5	10.5	10.4	0.34	.7973
2015	8.5	8.4	7.5	7.3	1.21	.1445	5.1b	6.2ab	5.9ab	6.4a	4.12	.0314	14.7	13.5	13.2	13.9	1.09	.3644
2016	6.1	5.8	5.6	5.0	1.42	.2522	4.9	4.9	5.2	5.2	0.21	.8816	11.0	10.7	10.2	10.8	0.38	.3169

Bold values represent a significant statistical difference was detected.

particularly pronounced in plots receiving high levels of N addition (3 g N m⁻² year⁻¹), which exhibited the greatest loss of canopy cover and shrub mortality, and had the lowest shrub cover in the final years of the study. We also observed increased woody litter production in shrubs subject to the highest level of N addition, which further reflects the increased shrub canopy dieback indicated by reduced shrub cover. This illustrates the potential for N deposition to exacerbate shrub loss during severe drought.

Nitrogen deposition may increase plant susceptibility to drought by stimulating higher rates of growth and productivity (Bobbink et al., 2010; Friedrich et al., 2012; Meyer-Grünefeldt et al., 2015). In European heathlands, for example, increases in shrub productivity under elevated N deposition have been found to increase plant susceptibility to other secondary factors, such as drought (Bobbink & Lamers, 2002). Our data suggest this may also occur in semiarid shrublands subject to N deposition. Many native CSS species, such as *A. californica*, are adapted to seasonal drought, losing their leaves during the summer dry season (Harrison, Small, & Mooney, 1971). However, with sufficient soil moisture, these species grow rapidly and exhibit high rates of gas exchange, which may result in increased susceptibility to xylem embolism (Jacobsen, Pratt, Davis, & Ewers, 2007; Kolb & Davis, 1994), and this could be especially true under high N conditions. Pivovarov et al. (2016) found that *A. californica* can be very physiologically responsive to N addition in the field, increasing rates of gas exchange and water use, which could increase susceptibility to cavitation and reduce water transport. The initial higher leaf litter production and increased leaf area observed in shrubs from high N plots demonstrate shrubs responded to N addition with increased growth and productivity. Higher leaf area in shrubs subject to high levels of N addition also likely increased physiological demand for water (Pivovarov et al., 2016), which could have depleted soil moisture more quickly, hastening the onset of water stress. The higher foliar N we observed in these shrubs further suggests that these shrubs may have been more physiologically active. The hypothesis of increased susceptibility to drought with increased productivity under high N conditions is further supported by $\delta^{13}\text{C}$ data showing shrubs in control plots exhibited higher WUE (Farquhar et al., 1989), relative to shrubs from high N addition plots. Reduced WUE during extended drought in shrubs subject to high N availability could have contributed to increased transpiration

rates and elevated water stress. Thus, it appears increased productivity and growth at the leaf level may have reduced shrub WUE and drought tolerance, eventually increasing canopy dieback and mortality of this species under elevated N availability.

In addition to increased susceptibility to drought, elevated N availability could have had other effects that influence the ability of shrubs to withstand prolonged drought. Nitrogen addition has been found to reduce root:shoot ratios in seedlings of *A. californica* (Valliere & Allen, 2016a), and this could also occur in mature shrubs. Grulke, Andersen, Fenn, and Miller (1998), for example, documented reduced root biomass in a tree species of southern California under chronic N deposition. Diversity and function of arbuscular mycorrhizae may also be negatively affected by N deposition (Egerton-Warburton & Allen, 2000; Sigüenza, Corkidi, & Allen, 2006). Mycorrhizae can play an important role in plant drought tolerance (Augé, 2001), and N-impacted soil communities may offer less protection against under drought in native CSS species such as *A. californica* (Valliere & Allen, 2016a). It is also possible that elevated soil N had a direct negative impact on native shrubs (Bobbink & Lamers, 2002). Both *A. californica* and *Encelia californica* Nutt., another drought-deciduous CSS shrub species, showed increased mortality when grown in soils with >80 $\mu\text{g N/g}$ for several months in a pot study (Allen et al., 2005), and we observed levels of N availability exceeding this amount in high N addition plots, although it is unlikely this high concentration extended beyond the soil surface (>10 cm).

Competition from nonnative annual species may have also negatively impacted native shrubs, especially in high N plots. These shallow-rooted annuals are more competitive for water, rapidly depleting soil moisture in the upper soil profile to the detriment of deeper-rooted perennials (Eliason & Allen, 1997; Wood et al., 2006). This effect could be even more pronounced under high N due to increased growth of nonnatives, as shown in this study. Wood et al. (2006), for example, found that annual grasses at high N deposition sites inhibited soil water percolation, depriving deeper-rooted natives of water. This altered ecohydrological response could be especially severe during periods of extended drought when water is extremely limiting, and be an important contributor to shrub loss and invasion under N deposition.

Resource availability often plays a key role in nonnative plant invasion (Davis et al., 2000), and N deposition has been shown to

increase invasion in multiple ecosystems (Brooks, 2003; Ochoa-Hueso, Pérez-Corona, & Manrique, 2013; Schwinning et al., 2005), including CSS (Allen et al., 2016; Cox et al., 2014). Here, we demonstrate that drought-induced shrub loss in conjunction with N addition may create a window of opportunity for nonnative species. Despite below-average rainfall, there was sufficient soil moisture each year to trigger germination of annual species, and nonnative annuals were particularly successful as the drought progressed, especially under high N. This was likely due in part to increased light availability with shrub canopy loss (Keeley, Baer-Keeley, & Fotheringham, 2005; Zedler, Gautier, & McMaster, 1983). Nonnative annual grasses and forbs may be successful under high N conditions and drought for a number of reasons. These species germinate earlier than native annuals and before most shrubs leaf out (Wainwright & Cleland, 2013), which provides first access to soil moisture and N. Nonnatives may also be more competitive for soil N and water, especially during drought (Elision & Allen, 1997; Everard, Seabloom, Harpole, & de Mazancourt, 2010). Finally, altered mycorrhizal diversity in N-impacted soils disproportionately benefits annual nonnatives (Egerton-Warburton & Allen, 2000; Sigüenza et al., 2006) including several of the dominant species we observed increasing under N addition at our site (Valliere & Allen, 2016b).

A major strength of this study is our inclusion of multiple levels of N addition in the experimental design that correspond to the range of N deposition rates that occur in the region, up to $30 \text{ kg ha}^{-1} \text{ year}^{-1}$ (Fenn et al., 2010; Tonnesen et al., 2007). This approach allowed us to detect changes in some ecological parameters at low levels ($5 \text{ kg ha}^{-1} \text{ year}^{-1}$), such as native herbaceous cover and biomass, while changes in other metrics such as shrub cover and mortality only manifested at the highest level of N addition ($30 \text{ kg ha}^{-1} \text{ year}^{-1}$). We predicted N addition would benefit nonnatives over natives, but it is somewhat surprising how quickly the plant community responded. The only previous N addition experiments in mature CSS shrublands did not yield increases in nonnative cover even at much higher rates of N application (Vourlitis & Pasquini, 2009). The rapid changes we report here were likely due to extreme drought conditions and a different species composition than in this previous study. For example, multiple nonnative annual species were already present at our site at the onset of the study, albeit in low numbers, while the plots described by Vourlitis and Pasquini (2009) were mostly devoid of such species. Further, our plots were dominated by a single shrub species, *A. californica*. It is possible that if other shrub species were present in higher numbers, they would have responded differently and compensated for the loss of *A. californica* cover. For example, Vourlitis and Pasquini (2009) found that *A. californica* declined over time with N addition while another species, *Salvia mellifera*, increased in abundance, although these results were reported prior to the recent drought.

While it seems likely that prolonged drought was primarily responsible for shrub loss during the study period, we did not include a water addition treatment in our experimental design, nor do we have vegetation data from years with average or

above-average rainfall. Thus, we cannot rule out other factors, natural or anthropogenic. However, our plant functional trait data suggest a role of plant–water relations in the response of native shrubs to N addition, and we did not observe signs of other stressors such as insects or disease when examining plant shoots or roots. Ambient N deposition at the site is also relatively low, and soil N availability was typical of a low N deposition site. Furthermore, previous work in this ecosystem, both correlative (Keeley, Fotheringham, & Baer-Keeley, 2006) and experimental (Kimball et al., 2014), has demonstrated a positive relationship between water availability and native shrub cover and establishment. Long-term monitoring of vegetation dynamics within these plots and future experiments manipulating both water and N will be useful in further elucidating patterns and mechanisms of shrub loss.

In conclusion, we show that chronic N deposition may drive native shrub loss and concomitant invasion of nonnative annuals during periods of extended drought. Addition of N may negatively impact native shrubs through increased productivity, resulting in reduced WUE and drought tolerance. Furthermore, the resulting shrub mortality and opening of the shrub canopy appear to create a window of opportunity for the invasion of nonnative plant species, potentially contributing to vegetation-type conversion. Anthropogenic N deposition, drought, and the invasion of nonnative species are major drivers of global change that are expected to increase in the future (Bradley, Blumenthal, Wilcove, & Ziska, 2010; Galloway, 2005; Giorgi & Lionello, 2008), and CSS and other Mediterranean-type ecosystems are predicted to be particularly vulnerable (Moreno & Oechel, 2012; Sala et al., 2000). This work highlights the potential for multiple components of global change to negatively impact these sensitive ecosystems and has important implications for ecosystem services and long-term conservation of Mediterranean-type shrublands.

ACKNOWLEDGEMENTS

This work was supported by the National Park Service Air Resource Division (TASK AGREEMENT NO. J8C07110022) and an NSF Doctoral Dissertation Improvement Grant (DEB-1501110). We would like to thank the many NPS employees, volunteers, graduate and undergraduate students who assisted in the field and laboratory and made this research possible.

REFERENCES

- Adams, H. D., Guardiola-Claramonte, M., Barron-Gafford, G. A., Villegas, J. C., Breshears, D. D., Zou, C. B., ... Huxman, T. E. (2009). Temperature sensitivity of drought-induced tree mortality portends increased regional die-off under global-change-type drought. *Proceedings of the National Academy of Sciences of the United States of America*, *106*, 7063–7066.
- Allen, M. F., Allen, E. B., Lansing, J. L., Pregitzer, K. S., Hendrick, R. L., Ruess, R. W., & Collins, S. L. (2010). Responses to chronic N fertilization of ectomycorrhizal pinon but not arbuscular mycorrhizal juniper in a pinon-juniper woodland. *Journal of Arid Environments*, *74*, 1170–1176.

- Allen, C. D., & Breshears, D. D. (1998). Drought-induced shift of a forest–woodland ecotone: Rapid landscape response to climate variation. *Proceedings of the National Academy of Sciences of the United States of America*, *95*, 14839–14842.
- Allen, E. B., Egerton-Warburton, L. M., Hilbig, B. E., & Valliere, J. M. (2016). Interactions of arbuscular mycorrhizal fungi, critical loads of nitrogen deposition, and shifts from native to invasive species in a southern California shrubland. *Botany-Botanique*, *94*(6), 425–433.
- Allen, C. D., Macalady, A. K., Chenchouni, H., Bachelet, D., McDowell, N., Vennetier, M., ... Hogg, E. T. (2010). A global overview of drought and heat-induced tree mortality reveals emerging climate change risks for forests. *Forest Ecology and Management*, *259*, 660–684.
- Allen, E. B., Padgett, P., Bytnerowicz, A., & Minnich, R. A. (1998). *Nitrogen deposition effects on coastal sage vegetation of Southern California*. Proceedings of the International Symposium on Air Pollution and Climate Change Effects on Forest Ecosystem.
- Allen, E. B., Sirulnik, A. G., Egerton-Warburton, L., Kee, S. N., Bytnerowicz, A., Padgett, P. E., ... Meixner, T. (2005). Air pollution and vegetation change in California shrublands. In BE Kus and JL Beyers (Technical Coordinators). *Planning for biodiversity: Bringing research and management together* (pp. 79–96). General Technical Report PSW-GTR-195. Albany, California, Pacific Southwest Research Station, Forest Service, US Department of Agriculture.
- Anderegg, W. R., Kane, J. M., & Anderegg, L. D. (2013). Consequences of widespread tree mortality triggered by drought and temperature stress. *Nature Climate Change*, *3*, 30–36.
- Asner, G. P., Brodrick, P. G., Anderson, C. B., Vaughn, N., Knapp, D. E., & Martin, R. E. (2016). Progressive forest canopy water loss during the 2012–2015 California drought. *Proceedings of the National Academy of Sciences of the United States of America*, *113*, E249–E255.
- Augé, R. M. (2001). Water relations, drought and vesicular-arbuscular mycorrhizal symbiosis. *Mycorrhiza*, *11*, 3–42.
- Bell, J. L., Sloan, L. C., & Snyder, M. A. (2004). Regional changes in extreme climatic events: A future climate scenario. *Journal of Climate*, *17*, 81–87.
- Bobbink, R., Hicks, K., Galloway, J., Spranger, T., Alkemade, R., Ashmore, M., ... De Vries, W. (2010). Global assessment of nitrogen deposition effects on terrestrial plant diversity: A synthesis. *Ecological Applications*, *20*, 30–59.
- Bobbink, R., & Lamers, L. (2002). 12 Effects of increased nitrogen deposition. In J.N.B. Bell & M. Treshow (Eds.), *Air pollution and plant life* (p. 201). West Sussex: John Wiley & Sons.
- Bradley, B. A., Blumenthal, D. M., Wilcove, D. S., & Ziska, L. H. (2010). Predicting plant invasions in an era of global change. *Trends in Ecology & Evolution*, *25*, 310–318.
- Breshears, D. D., Cobb, N. S., Rich, P. M., Price, K. P., Allen, C. D., Balice, R. G., ... Belnap, J. (2005). Regional vegetation die-off in response to global-change-type drought. *Proceedings of the National Academy of Sciences of the United States of America*, *102*, 15144–15148.
- Brooks, M. L. (2003). Effects of increased soil nitrogen on the dominance of alien annual plants in the Mojave Desert. *Journal of Applied Ecology*, *40*, 344–353.
- Coates, A. R., Dennison, P. E., Roberts, D. A., & Roth, K. L. (2015). Monitoring the impacts of severe drought on southern California chaparral species using hyperspectral and thermal infrared imagery. *Remote Sensing*, *7*, 14276–14291.
- Cox, R. D., Preston, K. L., Johnson, R. F., Minnich, R. A., & Allen, E. B. (2014). Influence of landscape-scale variables on vegetation conversion to exotic annual grassland in southern California, USA. *Global Ecology and Conservation*, *2*, 190–203.
- Dai, A. (2013). Increasing drought under global warming in observations and models. *Nature Climate Change*, *3*, 52–58.
- Dale, V. H., Joyce, L. A., McNulty, S., Neilson, R. P., Ayres, M. P., Flannigan, M. D., ... Peterson, C. J. (2001). Climate change and forest disturbances: Climate change can affect forests by altering the frequency, intensity, duration, and timing of fire, drought, introduced species, insect and pathogen outbreaks, hurricanes, windstorms, ice storms, or landslides. *BioScience*, *51*, 723–734.
- Daly, C., Halbleib, M., Smith, J. I., Gibson, W. P., Doggett, M. K., Taylor, G. H., ... Pasteris, P. P. (2008). Physiographically sensitive mapping of climatological temperature and precipitation across the conterminous United States. *International Journal of Climatology*, *28*, 2031–2064.
- Davis, M. A., Grime, J. P., & Thompson, K. (2000). Fluctuating resources in plant communities: A general theory of invasibility. *Journal of Ecology*, *88*, 528–534.
- De Marco, A., Proietti, C., Cionni, I., Fischer, R., Screpanti, A., & Vitale, M. (2014). Future impacts of nitrogen deposition and climate change scenarios on forest crown defoliation. *Environmental Pollution*, *194*, 171–180.
- Dukes, J. S., & Mooney, H. A. (1999). Does global change increase the success of biological invaders? *Trends in Ecology & Evolution*, *14*, 135–139.
- Egerton-Warburton, L. M., & Allen, E. B. (2000). Shifts in arbuscular mycorrhizal communities along an anthropogenic nitrogen deposition gradient. *Ecological Applications*, *10*, 484–496.
- Ehrenfeld, J. G. (2003). Effects of exotic plant invasions on soil nutrient cycling processes. *Ecosystems*, *6*, 503–523.
- Eliason, S. A., & Allen, E. B. (1997). Exotic grass competition in suppressing native shrubland re-establishment. *Restoration Ecology*, *5*, 245–255.
- Everard, K., Seabloom, E. W., Harpole, W. S., & de Mazancourt, C. (2010). Plant water use affects competition for nitrogen: Why drought favors invasive species in California. *The American Naturalist*, *175*, 85–97.
- Fahrenkamp-Uppenbrink, J. (2015). California drought worst in the past millennium. *Science*, *347*, 624.
- Farquhar, G. D., Ehleringer, J. R., & Hubick, K. T. (1989). Carbon isotope discrimination and photosynthesis. *Annual Review of Plant Biology*, *40*, 503–537.
- Fenn, M., Allen, E., Weiss, S., Jovan, S., Geiser, L., Tonnesen, G., ... Yuan, F. (2010). Nitrogen critical loads and management alternatives for N-impacted ecosystems in California. *Journal of Environmental Management*, *91*, 2404–2423.
- Fenn, M. E., Baron, J. S., Allen, E. B., Rueth, H. M., Nydick, K. R., Geiser, L., ... Neitlich, P. (2003). Ecological effects of nitrogen deposition in the western United States. *BioScience*, *53*, 404–420.
- Friedrich, U., von Oheimb, G., Kriebitzsch, W.-U., Schießelmann, K., Weber, M. S., & Härdtle, W. (2012). Nitrogen deposition increases susceptibility to drought—experimental evidence with the perennial grass *Molinia caerulea* (L.) Moench. *Plant and Soil*, *353*, 59–71.
- Galloway, J. N. (2005). The global nitrogen cycle: Past, present and future. *Science in China Series C-Life Sciences*, *48*, 669–677.
- Giorgi, F., & Lionello, P. (2008). Climate change projections for the Mediterranean region. *Global and Planetary Change*, *63*, 90–104.
- Griffin, D., & Anchukaitis, K. J. (2014). How unusual is the 2012–2014 California drought? *Geophysical Research Letters*, *41*, 9017–9023.
- Grulke, N., Andersen, C., Fenn, M., & Miller, P. (1998). Ozone exposure and nitrogen deposition lowers root biomass of ponderosa pine in the San Bernardino Mountains, California. *Environmental Pollution*, *103*, 63–73.
- Harrison, A., Small, E., & Mooney, H. (1971). Drought relationships and distribution of two Mediterranean-climate California plant communities. *Ecology*, *52*, 869–875.
- Haston, L., & Michaelsen, J. (1997). Spatial and temporal variability of southern California precipitation over the last 400 yr and relationships to atmospheric circulation patterns. *Journal of Climate*, *10*, 1836–1852.

- Hawkes, C. V., Wren, I. F., Herman, D. J., & Firestone, M. K. (2005). Plant invasion alters nitrogen cycling by modifying the soil nitrifying community. *Ecology Letters*, *8*, 976–985.
- Hobbs, R. J. (2000). *Invasive species in a changing world*. Washington, DC: Island Press.
- Jacobsen, A. L., Pratt, R. B., Davis, S. D., & Ewers, F. W. (2007). Cavitation resistance and seasonal hydraulics differ among three arid Californian plant communities. *Plant, Cell & Environment*, *30*, 1599–1609.
- Jones M. E., Paine T. D., Fenn M. E., Poth M. A. (2004). Influence of ozone and nitrogen deposition on bark beetle activity under drought conditions. *Forest Ecology and Management*, *200*, 67–76.
- Keeley, J. E., Baer-Keeley, M., & Fotheringham, C. (2005). Alien plant dynamics following fire in Mediterranean-climate California shrublands. *Ecological Applications*, *15*, 2109–2125.
- Keeley, J. E., Fotheringham, C., & Baer-Keeley, M. (2006). Demographic patterns of postfire regeneration in Mediterranean-climate shrublands of California. *Ecological Monographs*, *76*, 235–255.
- Kimball, S., Goulden, M. L., Suding, K. N., & Parker, S. (2014). Altered water and nitrogen input shifts succession in a Southern California coastal sage community. *Ecological Applications*, *24*, 1390–1404.
- Kolb, K. J., & Davis, S. D. (1994). Drought tolerance and xylem embolism in co-occurring species of coastal sage and chaparral. *Ecology*, *75*(3), 648–659.
- Loarie, S. R., Carter, B. E., Hayhoe, K., McMahon, S., Moe, R., Knight, C. A., ... Ackerly, D. D. (2008). Climate change and the future of California's endemic flora. *PLoS ONE*, *3*, e2502.
- Manea, A., Sloane, D. R., & Leishman, M. R. (2016). Reductions in native grass biomass associated with drought facilitates the invasion of an exotic grass into a model grassland system. *Oecologia*, *181*, 175–183.
- McDowell, N., Pockman, W. T., Allen, C. D., Breshears, D. D., Cobb, N., Kolb, T., ... Williams, D. G. (2008). Mechanisms of plant survival and mortality during drought: Why do some plants survive while others succumb to drought? *New Phytologist*, *178*, 719–739.
- Meyer-Grünefeldt, M., Friedrich, U., Klotz, M., Von Oheimb, G., & Härdtle, W. (2015). Nitrogen deposition and drought events have non-additive effects on plant growth—Evidence from greenhouse experiments. *Plant Biosystems—An International Journal Dealing With all Aspects of Plant Biology*, *149*, 424–432.
- Midgley, G., Hannah, L., Millar, D., Rutherford, M., & Powrie, L. (2002). Assessing the vulnerability of species richness to anthropogenic climate change in a biodiversity hotspot. *Global Ecology and Biogeography*, *11*, 445–451.
- Minnich, R. A., & Dezzani, R. J. (1998). Historical decline of coastal sage scrub in the Riverside-Perris Plain, California. *Western Birds*, *29*, 366–391.
- Mittermeier, R. A., Myers, N., Mittermeier, C. G., & Robles Gil, P. (1999). *Hotspots: Earth's biologically richest and most endangered terrestrial ecoregions*. CEMEX, SA, Agrupación Sierra Madre, SC.
- Moreno, J., & Oechel, W. C. (2012). *Global change and Mediterranean-type ecosystems*. New York, NY: Springer Science & Business Media.
- Mueller, R. C., Scudder, C. M., Porter, M. E., Talbot Trotter, R., Gehring, C. A., & Whitham, T. G. (2005). Differential tree mortality in response to severe drought: Evidence for long-term vegetation shifts. *Journal of Ecology*, *93*, 1085–1093.
- Myers, N., Mittermeier, R. A., Mittermeier, C. G., Da Fonseca, G. A., & Kent, J. (2000). Biodiversity hotspots for conservation priorities. *Nature*, *403*, 853–858.
- Ochoa-Hueso, R., Pérez-Corona, M. E., & Manrique, E. (2013). Impacts of simulated N deposition on plants and mycorrhizae from Spanish semiarid Mediterranean shrublands. *Ecosystems*, *16*, 838–851.
- Padgett, P. E., & Allen, E. B. (1999). Differential responses to nitrogen fertilization in native shrubs and exotic annuals common to Mediterranean coastal sage scrub of California. *Plant Ecology*, *144*, 93–101.
- Padgett, P. E., Allen, E. B., Bytnerowicz, A., & Minich, R. A. (1999). Changes in soil inorganic nitrogen as related to atmospheric nitrogenous pollutants in southern California. *Atmospheric Environment*, *33*, 769–781.
- Parker, S. S., & Schimel, J. P. (2010). Invasive grasses increase nitrogen availability in California grassland soils. *Invasive Plant Science and Management*, *3*, 40–47.
- Peñuelas, J., Lloret, F., & Montoya, R. (2001). Severe drought effects on Mediterranean woody flora in Spain. *Forest Science*, *47*, 214–218.
- Phoenix, G. K., Hicks, W. K., Cinderby, S., Kuylenstierna, J. C., Stock, W. D., Dentener, F. J., ... Gimeno, B. S. (2006). Atmospheric nitrogen deposition in world biodiversity hotspots: The need for a greater global perspective in assessing N deposition impacts. *Global Change Biology*, *12*, 470–476.
- Pivovarov, A. L., Santiago, L. S., Vourlitis, G. L., Grantz, D. A., & Allen, M. F. (2016). Plant hydraulic responses to long-term dry season nitrogen deposition alter drought tolerance in a Mediterranean-type ecosystem. *Oecologia*, *181*(3), 1–11.
- Sala, O. E., Chapin, F. S., Armesto, J. J., Berlow, E., Bloomfield, J., Dirzo, R., ... Kinzig, A. (2000). Global biodiversity scenarios for the year 2100. *Science*, *287*, 1770–1774.
- Schwinning, S., Starr, B. I., Wojcik, N. J., Miller, M. E., Ehleringer, J. E., & Sanford, R. L. Jr (2005). Effects of nitrogen deposition on an arid grassland in the Colorado Plateau cold desert. *Rangeland Ecology & Management*, *58*, 565–574.
- Sigüenza, C., Corkidi, L., & Allen, E. B. (2006). Feedbacks of soil inoculum of mycorrhizal fungi altered by N deposition on the growth of a native shrub and an invasive annual grass. *Plant and Soil*, *286*, 153–165.
- Simkin, S. M., Allen, E. B., Bowman, W. D., Clark, C. M., Belnap, J., Brooks, M. L., ... Gilliam, F. S. (2016). Conditional vulnerability of plant diversity to atmospheric nitrogen deposition across the United States. *Proceedings of the National Academy of Sciences of the United States of America*, *113*(15), 4086–4091.
- Sirulnik, A. G., Allen, E. B., Meixner, T., & Allen, M. F. (2007). Impacts of anthropogenic N additions on nitrogen mineralization from plant litter in exotic annual grasslands. *Soil Biology and Biochemistry*, *39*, 24–32.
- Talluto, M. V., & Suding, K. N. (2008). Historical change in coastal sage scrub in southern California, USA in relation to fire frequency and air pollution. *Landscape Ecology*, *23*, 803–815.
- Tonnesen, G. S., Wang, Z. W., Omary, M., & Vhien, C. J. (2007). *Assessment of nitrogen deposition: Modeling and habitat assessment*. California Energy Commission.
- Valliere, J. M. (2016). *Ecological impacts of nitrogen deposition, drought and nonnative plant invasion on coastal sage scrub of the Santa Monica mountains*. Doctoral dissertation. UC Riverside: Plant Biology. Retrieved from <http://escholarship.org/uc/item/7vp1961j>
- Valliere, J. M., & Allen, E. B. (2016a). Interactive effects of nitrogen deposition and drought-stress on plant-soil feedbacks of *Artemisia californica* seedlings. *Plant and Soil*, *403*(1–2), 1–14.
- Valliere, J. M., & Allen, E. B. (2016b). Nitrogen enrichment contributes to positive responses to soil microbial communities in three invasive plant species. *Biological Invasions*, *18*, 1–16.
- Vitousek, P. M., Aber, J. D., Howarth, R. W., Likens, G. E., Matson, P. A., Schindler, D. W., ... Tilman, D. G. (1997). Human alteration of the global nitrogen cycle: Sources and consequences. *Ecological Applications*, *7*, 737–750.
- Vourlitis, G. L., & Pasquini, S. C. (2009). Experimental dry-season N deposition alters species composition in southern Californian mediterranean-type shrublands. *Ecology*, *90*, 2183–2189.
- Vourlitis, G. L., Zorba, G., Pasquini, S. C., & Mustard, R. (2007). Chronic nitrogen deposition enhances nitrogen mineralization potential of semiarid shrubland soils. *Soil Science Society of America Journal*, *71*, 836–842.

- Wainwright, C. E., & Cleland, E. E. (2013). Exotic species display greater germination plasticity and higher germination rates than native species across multiple cues. *Biological Invasions*, *15*, 2253–2264.
- Wood, Y. A., Meixner, T., Shouse, P. J., & Allen, E. B. (2006). Altered ecohydrologic response drives native shrub loss under conditions of elevated nitrogen deposition. *Journal of Environmental Quality*, *35*, 76–92.
- Zedler, P. H., Gautier, C. R., & McMaster, G. S. (1983). Vegetation change in response to extreme events: The effect of a short interval between fires in California chaparral and coastal scrub. *Ecology*, *64*, 809–818.

How to cite this article: Valliere JM, Irvine IC, Santiago L, Allen EB. High N, dry: Experimental nitrogen deposition exacerbates native shrub loss and nonnative plant invasion during extreme drought. *Glob Change Biol.* 2017;00:1–13. <https://doi.org/10.1111/gcb.13694>

SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article.