

Altered water and nitrogen input shifts succession in a southern California coastal sage community

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Abstract. Vegetation-type conversions between grasslands and shrublands have occurred worldwide in semiarid regions over the last 150 years. Areas once covered by drought-deciduous shrubs in Southern California (coastal sage scrub) are converting to grasslands dominated by nonnative species. Increasing fire frequency, drought, and nitrogen deposition have all been hypothesized as causes of this conversion, though there is little direct evidence. We constructed rain-out shelters in a coastal sage scrub community following a wildfire, manipulated water and nitrogen input in a split-plot design, and collected annual data on community composition for four years. While shrub cover increased through time in all plots during the postfire succession, both drought and nitrogen significantly slowed recovery. Four years after the fire, average native shrub cover ranged from over 80% in water addition, ambient-nitrogen plots to 20% in water reduction, nitrogen addition plots. Nonnative grass cover was high following the fire and remained high in the water reduction plots through the third spring after the fire, before decreasing in the fourth year of the study. Adding nitrogen decreased the cover of native plants and increased the cover of nonnative grasses, but also increased the growth of one crown-sprouting shrub species. Our results suggest that extreme drought during postfire succession may slow or alter succession, possibly facilitating vegetation-type conversion of coastal sage scrub to grassland. Nitrogen addition slowed succession and, when combined with drought, significantly decreased native cover and increased grass cover. Fire, drought, and atmospheric N deposition are widespread aspects of environmental change that occur simultaneously in this system. Our results imply these drivers of change may reinforce each other, leading to a continued decline of native shrubs and conversion to annual grassland.

Key words: California, USA; coastal sage scrub; nonnative grasses; fire; global change; native plants; nitrogen; rain-out experiment; succession.

INTRODUCTION

Grasslands and shrublands occupy similar semiarid climatic zones around the globe, making conversions between the two habitats fairly common throughout these regions (Archer et al. 1995, Sankey et al. 2012). In many areas, native shrubs have encroached into grasslands, apparently due to increased livestock grazing and decreased fire frequency (Harrington 1991, Brown and Archer 1999, Van Auken 2000). In Californian drought-deciduous coastal sage scrub (CSS or “soft chaparral”) and in other mediterranean-climate shrublands around the globe, the opposite trend is observed, with a frequent conversion of native shrublands to systems dominated by a few invasive species, such as conversion of CSS to nonnative Eurasian grasslands (Stylinski and Allen 1999, Cione et al. 2002, Vila et al.

2003, Gaertner et al. 2009). In a 1998 study resampling the 1930s Vegetation Type Mapping (VTM) survey (Wieslander et al. 1933), Minnich and Dezzani documented that 18% of the area once covered by CSS was converted to grasslands dominated by Eurasian species, including *Bromus madritensis* and *Avena barbata* (Minnich and Dezzani 1998). A more recent study reported that 49% of the CSS plots identified by the VTM in the early 1930s had converted to Eurasian grassland by 2005 (Talluto and Suding 2008). Adjacent chaparral communities dominated by evergreen sclerophyllous shrubs at slightly higher elevations (“hard chaparral”) do not seem to be experiencing this conversion (Allen et al. 2005). Coastal sage scrub and other mediterranean-climate systems have been identified as biodiversity “hotspots” and have decreased in cover by direct land use changes for human activities, making vegetation-type conversions in remaining open space of critical concern (Kirkpatrick and Hutchinson 1980, Myers et al. 2000, Vila et al. 2003, Bonet 2004, Padilla et al. 2009,

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Sharma et al. 2010, Cortina et al. 2011, Cox and Allen 2011, Heelemann et al. 2012).

Increasing fire frequency, atmospheric nitrogen (N) deposition, and drought have all been cited as possible causes of conversions, and all are expected to become increasingly problematic in the future (Diaz-Delgado et al. 2002, Syphard et al. 2006, Wood et al. 2006, Seager et al. 2007, Stow et al. 2008, Klausmeyer and Shaw 2009, Fenn et al. 2010). Observational studies indicate the relative abundance of grassland and shrub species is influenced by fire frequency, with shrubs increasing in importance in undisturbed grasslands and grasses expanding in recently burned shrublands (Callaway and Davis 1993, DeSimone and Zedler 1999, Keeley 2002). Most of the dominant CSS shrubs, including *Artemisia californica*, *Salvia mellifera*, and *Eriogonum fasciculatum*, crown-sprout following fire. Some species also germinate from seed or, in the case of *Acmispon glaber*, regenerate solely from seed following fire (Keeley and Keeley 1984). Forbs and grasses increase in abundance in the first year following fire, and then decrease in cover as succession proceeds and shrub cover increases (Keeley et al. 2005b). Locations with a history of repeated fire at short intervals tend to have increased cover of nonnative grasses relative to locations that have experienced less frequent fire (Talluto and Suding 2008, Keeley and Brennan 2012). In other ecosystems invaded by nonnative grasses, the resulting grasslands burn more frequently than native systems due to high flammability of standing dead grass, leading to a positive feedback mechanism that forces the system toward a new stable state (Dantonio and Vitousek 1992, Vila et al. 2001, Ziska et al. 2005, Baker 2006).

The relative abundance of grass and CSS shrubs is also influenced by high levels of N deposition associated with atmospheric pollution (Allen et al. 2005). N deposition has greatly increased due to human activities, with levels of N deposition from 20–45 kg-ha⁻¹·yr⁻¹ in CSS adjacent to urban areas, and up to 145 kg-ha⁻¹·yr⁻¹ in heavily exposed areas, although this may be decreasing more recently (Phoenix et al. 2006, Vourlitis et al. 2009). The increase in soil N availability may favor nonnative grass species over native shrubs (Allen et al. 1998, Wood et al. 2006, Rao and Allen 2010), although experimental studies give conflicting results (Padgett and Allen 1999, Stylinski and Allen 1999, Wood et al. 2006). Community composition of CSS is altered in response to added N, but does not necessarily favor annuals over shrubs (Vourlitis et al. 2009).

A third factor influencing the abundance of shrubs and grasses is precipitation. Precipitation in mediterranean climates is highly variable from year to year (Jones 2000, Lana et al. 2006). This variability is expected to increase with global climate change, resulting in more intense storms and more extreme droughts (Jones 2000, Bell et al. 2004, Salinger 2005). Many CSS shrubs are summer deciduous, a strategy that allows them to avoid dry conditions (Harrison et al. 1971, Westman 1981).

During the wet season, CSS shrubs maintain high rates of gas exchange and exhibit rapid growth, constructing leaves and other tissues lost during the dry season (Harrison et al. 1971, Jacobsen et al. 2007, Rundel 2007). CSS shrubs have higher vulnerability to xylem cavitation than chaparral or desert shrubs, possibly making them susceptible to severe drought (Kolb and Davis 1994, Jacobsen et al. 2007, Lambrecht et al. 2011). Drought has been cited as one of the causes of CSS conversion to nonnative grassland (Heady 1988, Steers 2010). Restoration of degraded communities dominated by nonnative grasses back to CSS is more difficult during dry years (Cione et al. 2002). Precipitation and the amount of soil moisture are thought to influence total plant cover in CSS following fire, although the evidence is based on correlative studies. For example, increasing aridity, as indicated by annual solar insolation, was negatively correlated with shrub cover following fire (Keeley et al. 2005b). Shrub recruitment in postfire CSS and chaparral, as well as cover of herbaceous plants in postfire chaparral, were positively correlated with precipitation (Keeley et al. 1981, 2006).

Global change frequently involves multiple stressors that may have unexpected interactions, making it difficult to predict how natural communities will respond (Aber et al. 2001, Christensen et al. 2006). Although fire, N deposition, and drought are all considered to be important in causing vegetation-type conversions in CSS and other mediterranean-climate shrublands, there is surprisingly little direct evidence. Furthermore, all three aspects of global change are often correlated across the landscape or between years, complicating the interpretation of observational studies and pointing to the importance of factorial, manipulative experiments to understand how multiple factors will influence community composition (Zavaleta et al. 2003, Harpole et al. 2007, Ochoa-Hueso and Manrique 2010, Ochoa-Hueso et al. 2011). For example, air pollution within Southern California is correlated with distance from the coast, maximum temperature, and moisture, confounding studies based on geographic gradients (Talluto and Suding 2008). Knowledge of how fire, N deposition, and drought will influence CSS is critical because all factors are expected to increase in importance, and because mediterranean-type communities are already threatened by direct land conversion to human uses (Allen et al. 1998, Syphard et al. 2007, Klausmeyer and Shaw 2009).

Here, we evaluated the role of N deposition and drought in altering community composition in a postfire Southern California CSS community. Our research questions were: (1) How does altered water input influence CSS community recovery following a fire? (2) What is the influence of N deposition and are there interactions with water input? (3) Do water and N manipulations trigger vegetation-type conversion from CSS to grassland following fire? We hypothesized that drought would slow CSS recovery, N addition would

increase grass cover by giving grasses a competitive advantage over shrubs, and the two stressors would interact to influence community structure following fire. This is the first manipulative study we are aware of that investigates interactions between N deposition and precipitation on postfire CSS. Our results help clarify the effects of drought and N addition on succession in CSS and provide information critical to managing a threatened system in the context of global change.

METHODS

Study site

The study was conducted in the foothills of the Santa Ana Mountains, on Loma Ridge, within the Irvine Ranch National Landmark in Orange County, California, USA (117.704° W, 33.742° N). The climate is mediterranean, with an annual mean precipitation of 30 cm, which falls almost exclusively from November through April, and a predictable summer drought from May through October (Tustin Irvine Ranch weather 1902 to 2003; Western Regional Climate Center, data *available online*).⁶ The temperatures are moderate, with an average winter (November through April) high of 21.0°C and low of 6.2°C, and an average summer (May through October) high of 27.3°C and low of 13.1°C. Freezing temperatures are rarely observed at Loma Ridge. The study site is on a gently sloping, several meter deep colluvial deposit that has weathered from layers of sedimentary rock immediately southeast of the site. The soil is mapped as Myford Sandy Loam (California Soil Resource Lab, data *available online*).⁷ The vegetation is a mosaic of annual grassland and deciduous shrubland on the flat areas, and evergreen oaks in nearby ravines (Allison et al. 2013; M. L. Goulden et al., *unpublished manuscript*).

Fire history

The local ecosystem is fire prone; the study site burned in wildfires during 1914, 1948, 1967, 1998, and 2007 (CAL FIRE Fire and Resource Assessment Program, data *available online*).⁸ Our original experimental design included an explicit consideration of the effects of fire, which was applied as a controlled burn on half of the plots in February 2007. Ideally, the control burn would have been applied randomly to half the plots in each block, but due to safety and logistical constraints, the burn was applied to the northern half of the study area (to the plots that were near to each other on the landscape), leaving the southern half unburned. This original experimental design was altered on 22 October 2007, when all of the southern plots burned in the Santiago wildfire. Thus, half of the plots were burned in a prescribed fire in 6 February 2007, while the other half

of the plots burned during a high intensity wildfire on 22 October 2007 (Fig. 1). Any observed differences in plant community between the two areas may be due to the timing of the fires (February vs. October), the intensity of the fires, or other sources of spatial variation across the landscape. We initially included a contrast between the areas in our analyses, but this contrast was dropped because it was not significant (described in the *Data analysis* section below). We will focus on recovery following fire in general.

Experimental manipulations

We used a randomized split-plot design with eight replicate blocks consisting of three 18.29 × 12.19 m plots that received ambient, reduced (target 40% less), or increased (target 40% more) water input (Fig. 1). The experimental design is mirrored in a nearby annual grassland community, as described in Allison et al. (2013). We used steel Hi-Tunnels (Agratech, Pittsburg, California, USA) with retractable clear polyethylene roofs to remove ~40% of the annual precipitation from the reduced-water plots (see Plate 1). We accomplished this by closing the shelters during only a subset of the winter rains, thereby decreasing the number of storms that reached the reduced-water treatment. We based these decisions on forecasts from the National Weather Service's San Diego office. The roofs were otherwise retracted (they were in the off position for 94–96% of the year), which reduced potential artifact (measurements show no effect on air temperature or humidity when open). We biased shelter closure toward large storms, with a goal of reducing both storm intensity and frequency (M. L. Goulden et al., *unpublished manuscript*).

The water draining off the CSS shelters was collected with metal gutters and polyvinyl chloride (PVC) pipe, and stored in eight 11 360-L opaque polyethylene tanks, providing 5.09 cm of storage capacity. The water level in the tanks was monitored and recorded with pressure transducers and data loggers (Campbell Scientific, Logan, Utah, USA). This water was subsequently applied to the added-water plots using high-pressure gasoline-driven pumps (Davey Firefighter Plus 5.5 horsepower; Scoresby, Victoria, Australia), PVC pipe, and a dense network of pressure compensated drip tubing (Netafim Techline with 3.4 L/h pressure-compensated emitters every 30.5 cm at 25.4-cm intervals across each plot; Netafilm, Fresno, California, USA). Each added-water plot was equipped with a positive displacement water meter (Hersey 452, Cleveland, North Carolina, USA). The rainfall manipulation infrastructure was completed in April 2008 and operated beginning in the 2008–2009 wet season. Water occasionally spilled out of the storage tanks, so over the time period of the study, water reduction plots received 51% less water than ambient, and water addition plots received only 33% more than ambient plots (Fig. 2).

⁶ <http://www.wrcc.dri.edu>

⁷ <http://casoilresource.lawr.ucdavis.edu>

⁸ <http://frap.cdf.ca.gov/>

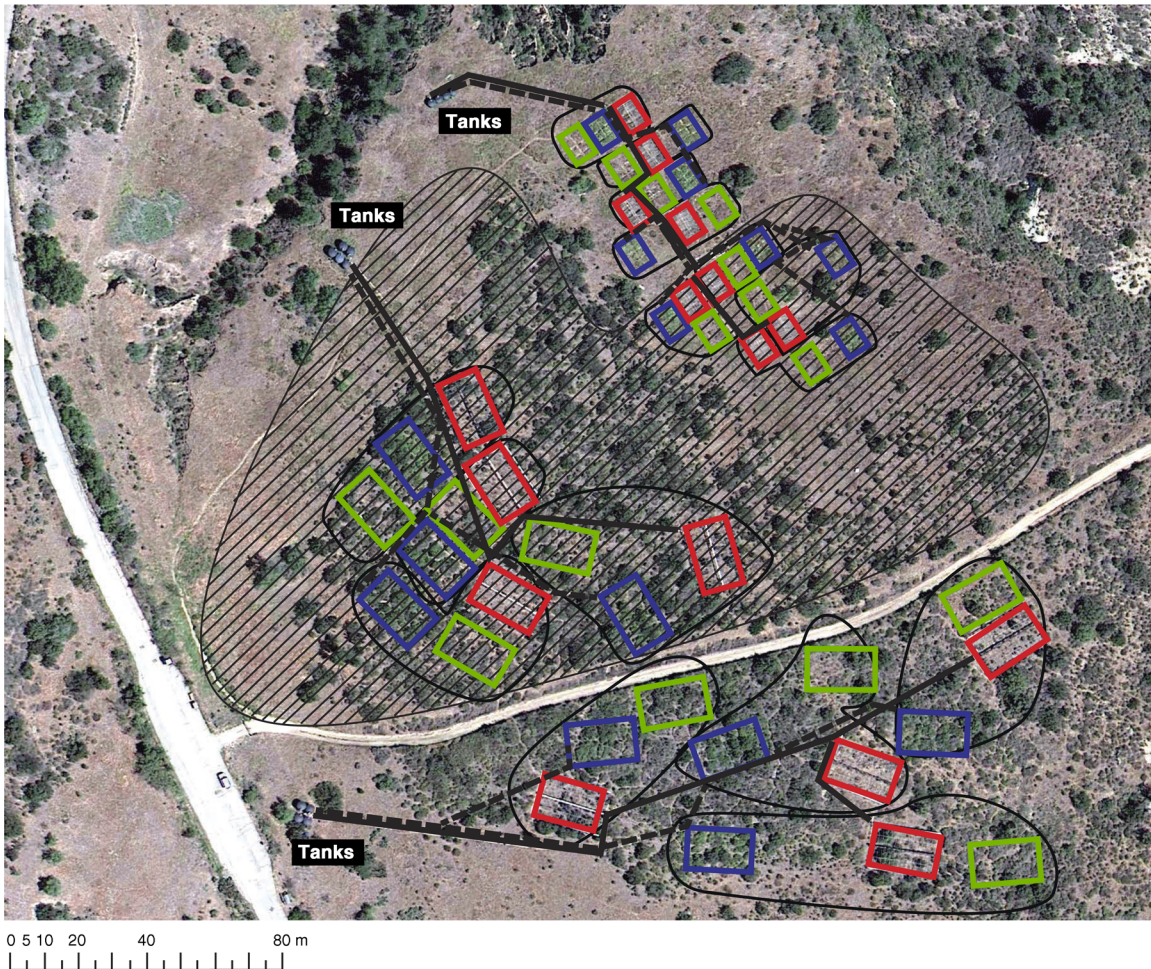


FIG. 1. Satellite image of the site in the Santa Ana Mountains, within the Irvine Ranch National Landmark in Orange County, California, USA, showing the larger coastal sage scrub (CSS) plots and the smaller plots in the adjacent annual grassland. Crosshatching indicates the area of the February 2007 control burn. Plots are coded by water treatment, with red indicating water reduction, green for ambient water, and blue for water addition. Thick dashed lines indicate water collection pipelines, and solid black lines indicate water distribution pipelines. The black-outlined polygons indicate blocks containing all treatment combinations. Each plot (rectangle) was divided in half lengthwise, and N treatments (ambient or added) were randomly assigned.

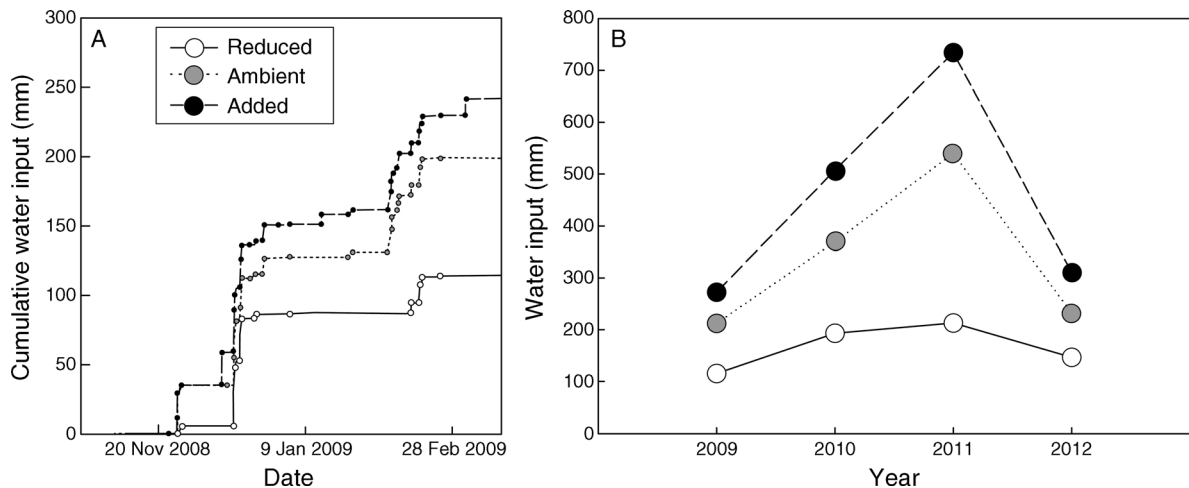


FIG. 2. (A) Cumulative water input during the 2008–2009 wet season for the three water treatments (reduced, ambient, and added). (B) Total water input for each growing season, indicated as the year when the season ended.

The water treatments were crossed with the presence or absence of N addition in a split-plot design (Fig. 1). Nitrogen deposition at our study site is $\sim 1.5 \text{ g}\cdot\text{m}^{-2}\cdot\text{yr}^{-1}$ (Fenn et al. 2010). N addition plots received $6 \text{ g}\cdot\text{m}^{-2}\cdot\text{yr}^{-1}$ of added N, an amount selected to simulate areas that have received higher deposition for several years and to push the system towards N saturation. The first 2 g were applied immediately prior to the first storm of the season (usually in October), as quick-release calcium nitrate (15.5% N, 0% P, 0% K, 19% Ca) to simulate the flush of N that occurs at the beginning of the rainy season. The remaining 4 g were applied approximately one month into the growing season (typically in December) as slow-release (four-month) calcium nitrate (14% N, 0% P, 0% K, 17% Ca). We added N as nitrate, rather than ammonia, because our objective was to study how N deposition influenced plants and not to study the process of nitrification. Nitrate is commonly used in experimental manipulations of N deposition (LeBauer and Treseder 2008).

Water input

The cumulative water input was calculated by combining precipitation measurements made with tipping bucket rain gauges (Texas Electronics 525, Dallas, Texas, USA; or Met One 360, Grants Pass, Oregon, USA) with the water removed or added in the treatments. The water input to the ambient treatment was taken as the precipitation measured by the rain gauge; the water input to the dry treatment was taken as the precipitation measured by the rain gauge during periods when the shelters were open; and the water input to the wet treatment was taken as the precipitation measured by the rain gauge plus the water input measured by the positive displacement water meters.

Water treatments were effective at altering water input in each year of the study (Fig. 2). The ambient rainfall in 2010 was close to the long-term mean annual mean (300 mm from 1928 to 2003 at the Irvine Ranch headquarters in Tustin, California, 7.6 km west of Loma Ridge). Precipitation increased from 2009 to 2011, and decreased in the final year (2012; Fig. 2). Water input in the water reduction plots was below the long-term average in all years of the study, while the added-water plots received lower than average in 2009 and 2012, but well above average in 2010 and 2011.

Species composition and shrub demography

Percent cover was determined by dividing each plot into 64 0.25-m^2 subplots and noting species presence in each subplot. The number of subplots that each species occupied was recorded and multiplied by 0.25 m^2 to calculate the total percent cover of that species in the total plot. Plants that occupied less than one subplot were recorded as $<1.6\%$ cover.

Crown-sprouting individual shrubs of three abundant species (*Artemisia californica*, *Malosma laurina*, and *Salvia mellifera*) were tagged in October 2008 to follow

survival and growth. The shrubs were randomly selected at six points along each of two diagonal transects established through each plot and at two points along two shorter transects spanning the width of each plot. Length and width were measured on an average of 34 tagged shrubs per plot. Shrub area was estimated using length and width ($\pi \times [\text{length} + \text{width}/4]^2$). The same individuals were re-visited each year to record survivorship and growth. Relative growth rate was calculated as the slope of relative total area per plot (total area in each year/total area in first year) through time with linear regression. Only individuals that survived through 2012 were included in calculations of relative growth rate.

Data analysis

We used mixed model, repeated-measures ANOVAs with water, N, and the interaction between water and N as fixed factors, and with block and the block \times water interaction as random factors (which takes into account the split-plot design), and year as a repeated factor to determine whether the system differed in total percent cover of shrubs vs. grasses through time (SAS version 9.3; SAS Institute 2011). We used the first order autoregressive covariance structure in the REPEATED statement of the model because it treats successive years as being more correlated and allows correlations to decline exponentially with time (Keselman et al. 1998). The same method was used to analyze percent cover (arcsine-transformed) of the five species that were strongly correlated with ordination space ($r^2 > 0.25$ with one or more axes in the ordination) to determine species-specific response to N and water manipulations. Percent cover of native forbs was also analyzed with this method.

Species composition data were analyzed by ordination, implemented with PC-ORD, to understand how composition of the entire community varied in plots over time (McCune and Mefford 1999). We used nonmetric multidimensional scaling (NMMDS) on Bray-Cutis distances to find the three-dimensional ordination in which the graphic distances from one plot to the next represent the dissimilarities in species composition. We also calculated correlations of secondary variables and of species with ordination space. We calculated the mean plot values for each water, N, and year treatment combination to visualize the trajectory of plots through time in species space.

While the repeated-measures ANOVAs and the ordination allowed us to investigate changes in species cover and community composition through time, it is also useful to look at composition several years after the fire to determine whether N and precipitation manipulations ultimately resulted in different types of communities. To address this question (number 3 in the *Introduction*), we analyzed percent cover in 2012 (four years postfire) of all shrubs, all grasses, all natives, and all nonnatives (See Appendix: Table A1 for a list of species belonging to each group). Note that native as

well as nonnative grasses occur in this system and some species were included in more than one analysis. Data were analyzed by ANOVAs using Proc GLM in SAS. Water and N treatment were included as fixed factors, block was a random factor, and all interactions were included in the model. The effects of water and block were tested over the water \times block interaction to take the split-plot nature of the design into account. We initially included a contrast statement in the model to compare the four blocks that were burned in the control burn to those that burned during the wildfire. In all cases, this contrast was highly nonsignificant ($P > 0.6$), so we do not present those results.

We used the program PRIMER (Clarke and Gorley 2006) to conduct permutational multivariate analysis of variance (PERMANOVA) of Bray-Curtis distance measures on percent cover in the final year of the study (2012), to understand post-succession composition of the entire community caused by the N and water manipulations. PERMANOVA partitions the variability in the distance matrix according to the sampling design and tests for significance through permutation (Anderson and ter Braak 2003). Our model included water treatment, N treatment, and the interaction between the two as fixed factors and block and the water \times block interaction as random factors. The distance matrix was permuted 999 times and type III SS were used in significance tests.

Finally, we used a GLM (Proc Glimmix in SAS with a logit link) to test whether survival through 2012 of the three marked shrub species (*Artemisia californica*, *Malosma laurina*, and *Salvia mellifera*) varied with water treatment, N treatment, or the interaction between the two. We included block and the block \times water interaction as random factors in the analysis. We compared the relative growth rates of each species in all plots with Proc GLM with water, N, and the interaction between the two as fixed factors and block and the water \times block interaction as random factors. The effects of water and block were tested over the water \times block interaction. We calculated total expansion of each species as survivorship \times relative growth rate to understand how survivorship and growth influenced patterns of change in cover through time. To allow for comparisons between the demographic data set and the data on total percent cover, we also calculated the increase in total cover of *Artemisia californica*, *Malosma laurina*, and *Salvia mellifera* as the slope of percent cover through time with linear regression.

RESULTS

Patterns of community composition through time

Large shifts in species composition occurred with fire recovery through time and varied with water and N treatment (Fig. 3). Shrub cover increased rapidly through time in the ambient and added-water plots, and at a slower pace in the reduced-water plots (water \times year interaction, $F_{6,147} = 8.71$, $P < 0.0001$). Shrub cover

was greatest in the added-water plots, intermediate in the ambient plots, and lowest in the water reduction plots (water $F_{2,14} = 30.48$, $P < 0.0001$; Appendix: Tables A1 and A2). Shrub cover was higher in the ambient-N plots compared to the added-N plots (N, $F_{1,147} = 6.72$, $P = 0.0105$; Appendix: Tables A1 and A2), and there was no interaction with water input (N \times water, $F_{2,147} = 0.47$, $P = 0.624$). Grass cover remained high through 2011 in the reduced-water plots, but decreased in the ambient and added-water plots (water \times year interaction, $F_{6,147} = 4.85$, $P = 0.0002$; Table 1), and decreased in all plots in 2012 (Fig. 3; Appendix: Tables A2 and A3). Cover of native forbs peaked at 20% immediately following the fire and gradually decreased to 3.4% through time. Native forb cover was not significantly altered by water or N manipulations (Appendix: Tables A2 and A3).

The ordination of plots in species space indicated community composition differed with water treatment and year of measurement (Fig. 4A, B), and that the postfire successional pattern differed with water and N treatment (Fig. 4C, D). Axis 1 in the ordination was positively correlated with the amount of water received by each plot in a year and native shrub cover, axis 2 was positively correlated with time since fire and native shrub cover, and axis 3 was positively correlated with abundance of nonnatives and negatively correlated with abundance of natives, especially *Acmispon glaber* (Table 1, Fig. 4A, B; Appendix: Table A4). The water-reduction plots grouped together based on species composition at the low values along axis 1 (low amounts of water received), and at high values along axis 3 (high cover of nonnatives). The ambient and added-water plots grouped together with high axis 1 and low axis 3 scores (low cover of nonnatives and high amounts of water received; Fig. 4B, D). Grass cover was negatively correlated with axis 1 (Table 1), and cover of nonnative grasses was negatively correlated with axis 2 (Table 1). Plots did not cluster according to N treatment along the first two axes, and N addition tended to shift composition along axis 3 (towards increased nonnative cover; Fig. 4D).

Species composition shifted from low values on axes 1 and 2 to high values on both axes through time (Fig. 4C). The water reduction treatment effectively slowed succession, such that these plots did not experience a decrease in grass cover until the final year of the study (2012), while species composition in the water addition plots shifted more quickly along axis 1, likely due to decreased grass cover in 2011 (Fig. 4C).

Species responses to environmental manipulations through time

Cover of the nonnative *Bromus madritensis*, the most abundant grass, was significantly higher in the reduced-water and added-N plots (water, $F_{2,14} = 9.16$, $P = 0.0029$; N, $F_{1,147} = 10.61$, $P = 0.0014$; Fig. 5). In contrast, the native perennial grass, *Stipa lepida*, had high cover in all

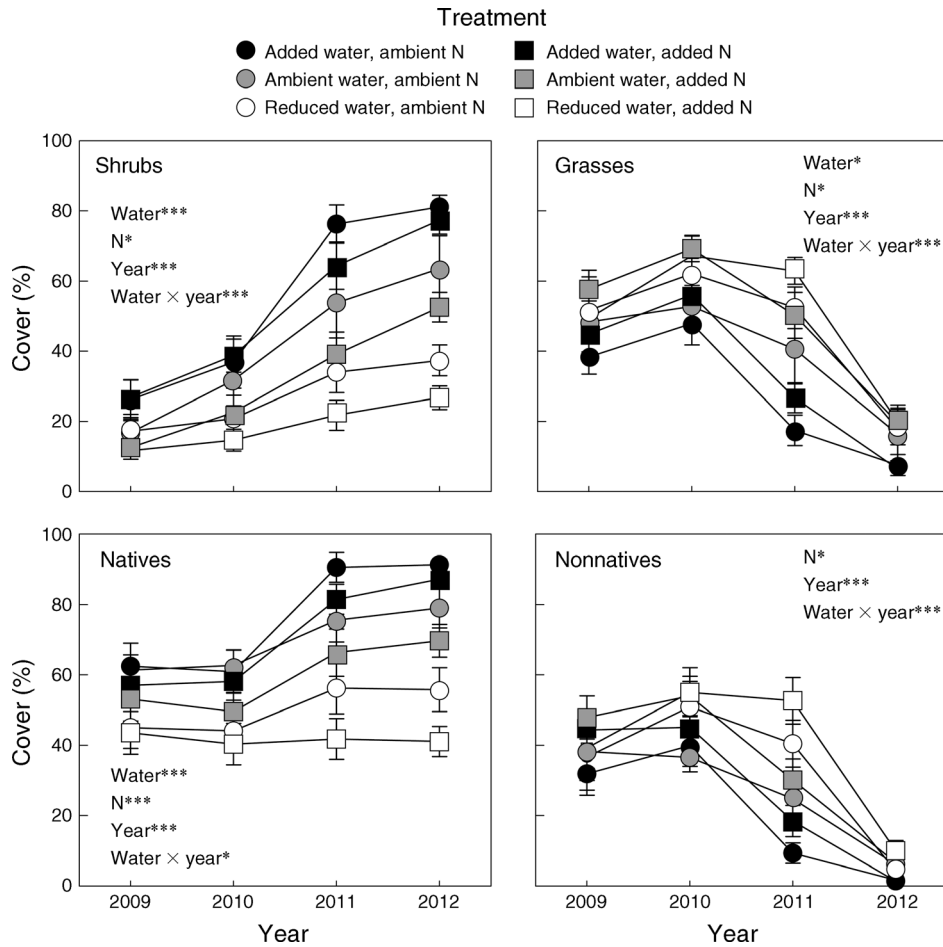


FIG. 3. Cover of shrubs, grasses, natives, and nonnatives in the different water and N treatments through time. Values are means \pm SE.
* $P < 0.05$; *** $P < 0.001$; nonsignificant factors are not listed.

plots (highest in added-water and ambient-N plots) in the year after the fire, and very low cover in all plots in 2011 and 2012 (Fig. 5; Appendix: Tables A2 and A3). The native N-fixing shrub, *Acmispon glaber*, increased through time in the ambient and added-water plots, but not in the reduced-water plots (water \times year interaction, $F_{6,147} = 3.33$, $P = 0.0042$; Fig. 5). Cover of the native shrub *Salvia mellifera* was higher in the added-water plots than in the reduced-water plots (water, $F_{2,14} = 5.29$, $P = 0.0125$; Appendix: Tables A2 and A3).

Demographic data on crown-sprouting shrubs indicated overall shrub expansion was lowest in the water reduction treatments for all species except *Artemisia californica* with added N (Fig. 6). Expansion was greatest in the ambient-water, added-N plots for *Artemisia californica*, and in the added-water, added-N plots for both *Malosma laurina* and *Salvia mellifera*, which corresponded with the linear increase in cover for each species as calculated from data on total percent cover (Fig. 6). Water and N treatments resulted in variation in survivorship for *Salvia mellifera* and

variation in relative growth rate (RGR) for *Malosma laurina*. While the proportion of plants that survived from 2008 through 2012 did not vary depending on treatment for *Artemisia californica* or *Malosma laurina*, survival of *Salvia mellifera* was significantly higher in the added- and ambient-water than in the reduced-water

TABLE 1. Pearson correlation coefficients (r) for environmental variables and major functional groups with the three ordination axes.

Variables	Axis 1	Axis 2	Axis 3
Forbs	-0.42	-0.321	-0.158
Grasses	-0.626	-0.749	0.254
Natives	0.486	0.55	-0.666
Nonnatives	-0.476	-0.883	0.289
Rain days	0.503	0.167	-0.481
Shrubs	0.805	0.559	-0.463
Water input	0.389	0.043	-0.452
Year	0.497	0.639	0.009

Notes: Variables are listed in alphabetical order. Correlations of all species with ordination space are listed in Appendix: Table A1.

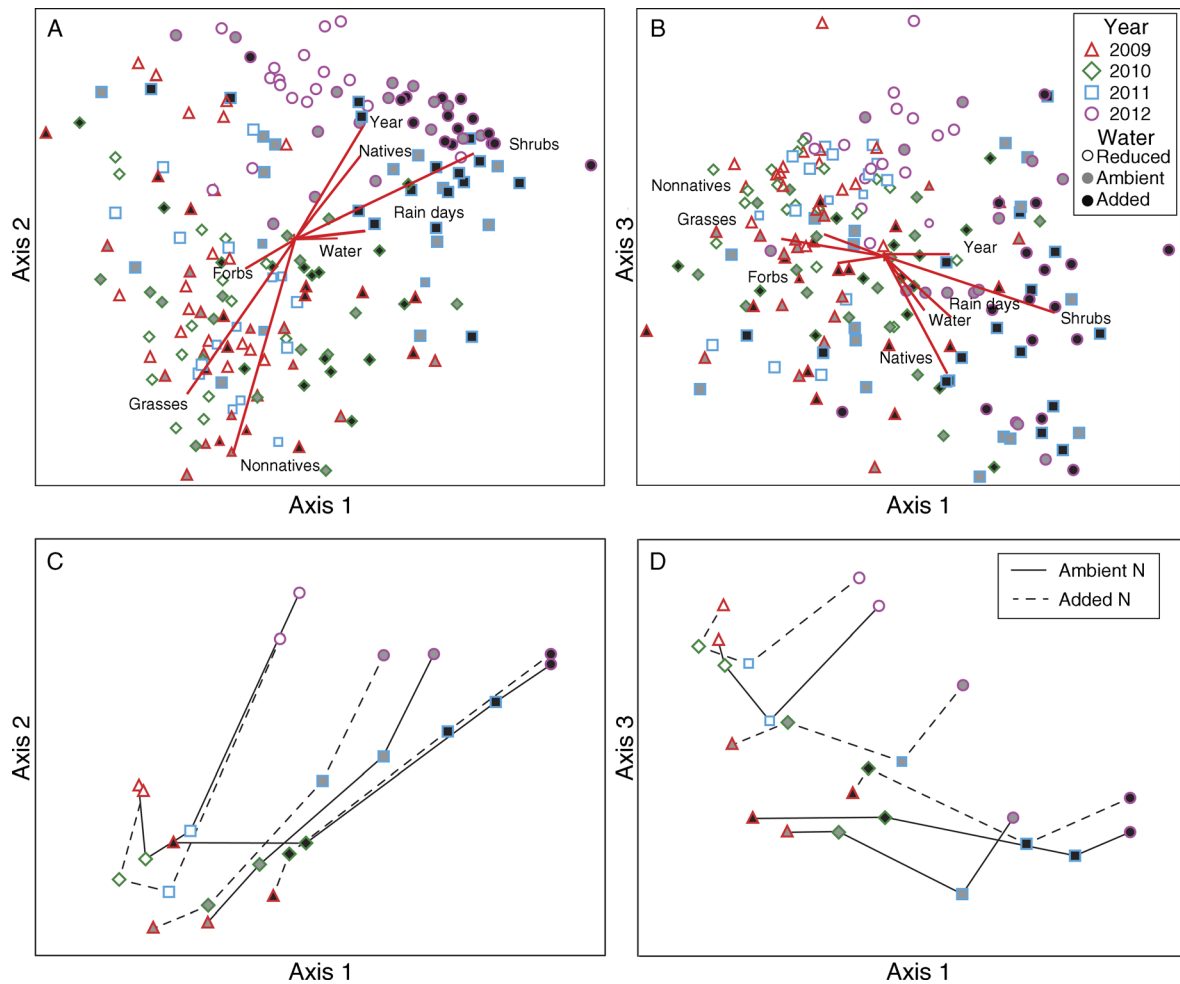


FIG. 4. Ordination of plots, coded by year and water input, based on species cover. Correlations of species with ordination space are listed in Appendix: Table A3. Bray-Curtis distance measures were used. (A) Axes 1 and 2 of the ordination, with vectors representing correlations between abundance of major functional groups of plants (grasses, shrubs, forbs, native, and nonnatives), year, and precipitation and rain days with axes of the ordination. The length of the vector represents the strength of the correlation. (B) Axes 1 and 3 of the ordination. (C) Average plot values for axes 1 and 2 of the ordination each water–N plot combination, with lines connecting the same plots measured in different years to show the trajectory of plots through time in species space. Solid lines connect ambient N plots, and dotted lines connect plots with added N. (D) Average water and N plot values for axes 1 and 3.

plots, and higher in the added-N than in the reduced-N plots (Appendix: Table A5). Relative growth rate from 2008 through 2012 of individuals that survived through 2012 was significantly higher in the added-water and ambient-water plots than in the reduced-water plots for *Malosma laurina*, while RGR of *Artemisia californica* and *Salvia mellifera* was similar in all water treatments. RGR was higher in the added-N plots for *Malosma laurina*, but only when water was also added. RGR of *Artemisia californica* and *Salvia mellifera* were similar in added-N and ambient-N plots (Appendix: Table A5).

Species composition after four years of postfire manipulations

Species composition four years after fire (in 2012) varied with water and N treatment. Mixed-model ANOVAs indicated that shrub cover differed signifi-

cantly depending on water and N treatment, with lowest cover in the reduced-water and added-N plots, and highest cover in the added-water plots (Table 2). In contrast, grass cover did not significantly differ depending on treatment. The cover of all native plants was highest in the added-water plots, followed by the ambient-water plots, and lowest in the reduced-water plots (Fig. 3, Table 2). Native cover was highest in the ambient-N plots (Fig. 3, Table 2). The cover of nonnative plants was higher in the water-reduction plots than in the ambient- or added-water plots (Fig. 3, Table 2).

According to the PERMANOVA, community composition in the final year of the study varied depending primarily on water (Pseudo $F_{2,47} = 6.08$, $P = 0.001$), but also on random variation in space (block Pseudo $F_{7,47} = 2.67$, $P = 0.002$). N did not have a significant effect on

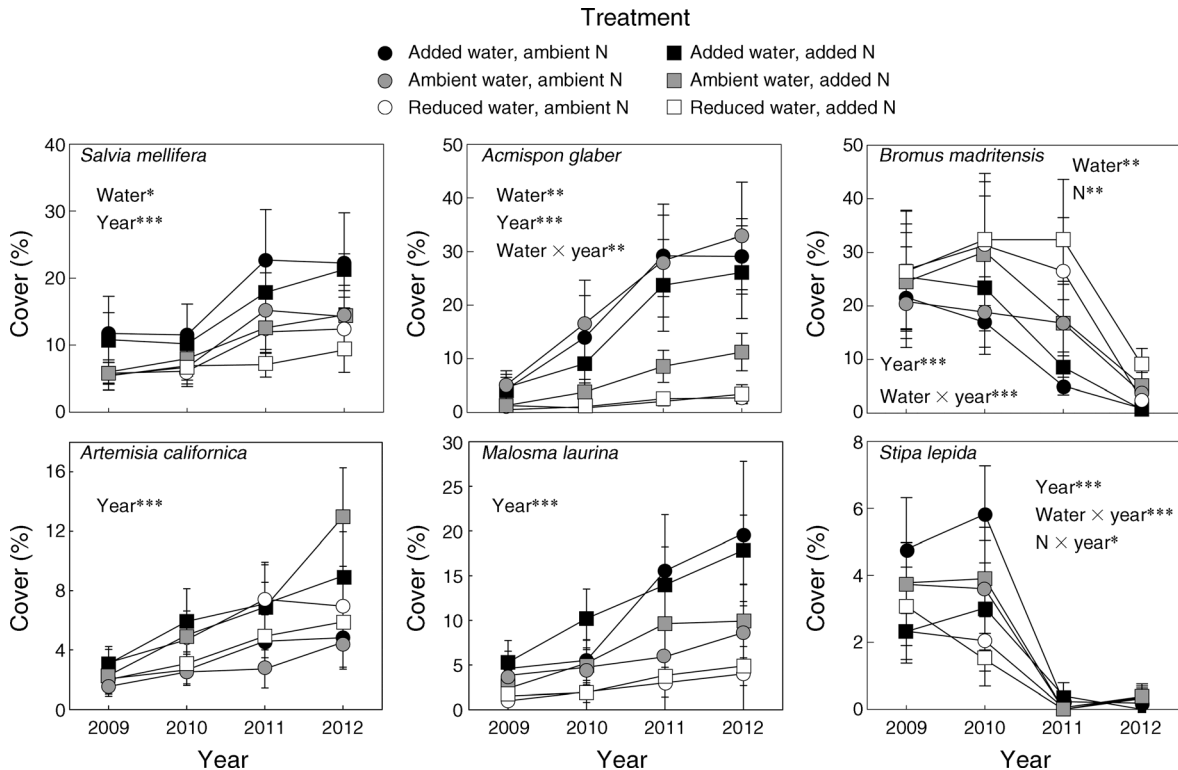


FIG. 5. Cover of *Salvia mellifera* (native deciduous shrub), *Malosma laurina* (native evergreen shrub), *Artemisia californica* (native deciduous shrub), *Acmispon glaber* (native, N-fixing shrub), *Bromus madritensis* (nonnative annual grass), and *Stipa lepida* (native perennial grass), in the different water and N treatments through time. Values are means \pm SE.

* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$; nonsignificant factors are not listed.

community composition in this year of the study (N , $F_{1,47} = 1.66$, $P = 0.123$). The interactions were not significant (Appendix: Table A6).

DISCUSSION

We have documented shifts in community composition following fire with reduced water and added N, three important aspects of global change to mediterranean-climate shrublands (Cione et al. 2002, Sharma et al. 2010, Ochoa-Hueso et al. 2011). Although fire is a natural part of mediterranean-climate systems such as Southern California CSS communities, it is still an extreme event, requiring crown-sprouting or germination of all plants, and the postfire community may be especially vulnerable to vegetation-type conversion (Zedler et al. 1983, Diaz-Delgado et al. 2002, De Luis et al. 2006). High cover of nonnative grasses following fire may increase fire frequency, which can lead to permanent vegetation-type conversion of shrublands to grasslands (D'Antonio and Vitousek 1992, Ziska et al. 2005). Our results indicate that fire followed by drought resulted in a community with a comparatively high cover of nonnative grasses and low cover of native shrubs (relative to ambient and added-water plots). Nitrogen addition following fire also significantly increased cover of nonnative grasses and decreased

cover of natives, but did not, without drought, shift community composition to $<50\%$ native shrub cover during the study (Fig. 3).

Reduced water input slowed shrub recovery and increased nonnative grass cover

Recovery of native shrubs from fire was generally delayed and diminished with reduced water input. Native shrubs recovered under ambient conditions, consistent with other studies demonstrating postfire crown-sprouting and seed germination (Keeley and Keeley 1984, Malanson and Westman 1985, Keeley et al. 2005b). The slower increase in cover of native shrubs in the reduced-water plots and the faster recovery in the added-water plots supports previous reports that recovery of shrub cover during succession was correlated with precipitation (Keeley et al. 2005b).

Many shrubs in CSS and other mediterranean-climate shrublands crown-sprout following fire, and they may be especially vulnerable during this sprouting period, as high gas exchange rates are needed to rebuild tissue (Desouza et al. 1986, Enright et al. 2011). Our results indicate both increased mortality and reduced growth of crown-sprouting individuals in the water reduction treatments. Crown-sprouting CSS shrubs tend to grow rapidly and produce large inflorescences following fire

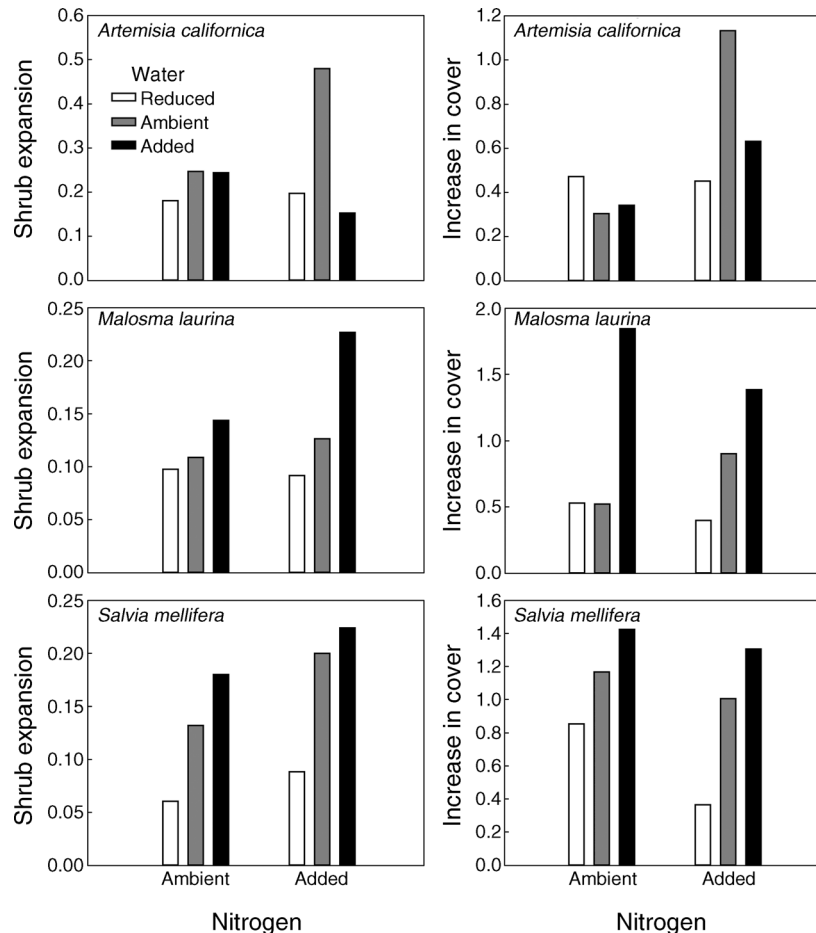


FIG. 6. Expansion of *Artemisia californica*, *Malosma laurina*, and *Salvia mellifera* in the different water and N treatments. Graphs on the left indicate shrub expansion of tagged crown-sprouting individuals, calculated as survivorship \times relative growth rate. Graphs on the right indicate the increase in cover of each species calculated by linear regression for each plot as the slope of percent cover over time.

(Rundel 2007), which may result in greater water requirements (Lambrecht et al. 2011). Decreased water availability likely led to the lower RGR of *Malosma laurina* and decreased survivorship of *Salvia mellifera* in water reduction plots. Although *Salvia mellifera* is known to adjust the size and longevity of its leaves depending on water availability, it is also vulnerable to xylem cavitation (Kolb and Davis 1994, Lambrecht et al. 2011), which may explain why survivorship was significantly lower for crown-sprouts in water-reduction plots.

The decreased shrub cover in the water-reduction plots may also have reflected decreased shrub recruitment in those plots. The greatly reduced cover of *Acmispon glaber*, a species that germinates from seed following fire, suggests that vulnerability at the establishment phase likely contributed to the delayed and decreased shrub recovery in water-reduction plots. Other studies of postfire shrub germination in mediterranean-climate systems have noted high mortality of seedlings during initial establishment (Tyler 1996,

Santana et al. 2012). It is also possible that *Acmispon glaber* individuals had slower growth rates in water-reduction plots, although we did not observe seedlings of any shrubs in the dry plots.

Some native species (such as the grass *Stipa lepida*), increased in cover immediately after the fire in all plots, but gradually declined (Fig. 3), in a fire-following pattern (Keeley 1991). Forbs also followed this pattern, presumably due to increased seed germination and reduced light competition during the first season postfire (Keeley 1991, Moreno and Oechel 1991). High cover of all herbaceous species, including nonnative grasses, in the first year of our study (Fig. 3) corresponds with previous reports (Keeley et al. 2005b). Nonnative grasses continued to have high cover (>50%) in water-reduction and ambient-water plots through 2011 (Fig. 3). Nonnative grasses experienced reduced cover in all plots in 2012. This may be due to lower precipitation in that year (Fig. 3), or it may be part of a long-term successional decline in herbaceous plants (Fig. 4).

TABLE 2. Results of mixed-model ANOVAs on the final cover of shrubs, grasses, natives, and nonnatives.

Variable and source	df	Type III SS	MS	F	P
All shrubs					
Water	2	17 888.13	8944.06	45.39	<0.0001
Block	7	2 367.79	338.26	1.72	0.184
Water × block	14	2 758.83	197.06	1.02	0.468
N	1	862.55	862.55	4.48	0.046
N × water	2	132.05	66.02	0.34	0.714
All grasses					
Water	2	1 385.94	692.97	3.04	0.080
Block	7	1 267.10	181.01	0.8	0.604
Water × block	14	3 186.59	227.61	1.87	0.094
N	1	23.32	23.32	0.19	0.666
N × water	2	40.26	20.13	0.17	0.848
Natives					
Water	2	13 676.86	6838.43	56.77	<0.0001
Block	7	3 051.40	435.91	3.62	0.019
Water × block	14	1 686.45	120.46	1.22	0.332
N	1	1 057.68	1 057.68	10.71	0.004
N × water	2	226.59	113.30	1.15	0.337
Nonnatives					
Water	2	300.98	150.49	4	0.042
Block	7	397.17	56.74	1.51	0.242
Water × block	14	526.53	37.61	1.41	0.231
N	1	47.05	47.05	1.77	0.198
N × water	2	87.03	43.51	1.63	0.219

Added N input also slowed shrub recovery and increased nonnative grass cover

Native shrub recovery was significantly reduced in the plots with added N, consistent with correlative studies suggesting decreased native cover in areas with high N deposition (Padgett and Allen 1999, Rundel 2007, Talluto and Suding 2008, Sharma et al. 2010). Despite the reduction in shrub recovery in the added-N plots, data on tagged individuals indicated that crown-sprouting individuals of *Salvia mellifera* had increased survivorship in the added-N plots. N also increased growth of *Malosma laurina* individuals, although only in the ambient and added-water plots. This suggests that the decreased cover of natives in the added-N plots is primarily due to a reduction in establishment of native shrub seedlings, possibly due to competition with nonnative annual grasses that increased in cover with added N. In another study, germination and survival of *Artemisia californica* was negatively correlated with nonnative grass cover (Eliason and Allen 1997). Here, tagged individuals of *A. californica* were not significantly influenced by N addition, but the cover of all native shrubs combined (including seedlings) was lower in the added-N plots (Fig. 3). The reduced native shrub cover in the N addition plots may primarily represent decreased establishment and growth of the native, N-fixing shrub, *Acmispon glaber*, in that treatment (Fig. 5).

The cover of the most abundant nonnative, *Bromus madritensis*, was significantly higher in the added-N plots than in the ambient-N plots, while natives showed the reverse pattern. This result supports the hypothesis

that invasive grasses have invaded CSS and other mediterranean-climate systems partially due to a greater ability to increase growth in response to N addition (Talluto and Suding 2008, Fenn et al. 2010, Sharma et al. 2010). One possible mechanism is that N addition appears to decrease the amount of arbuscular mycorrhizal (AM) fungi that colonizes roots of natives while not impacting the endophytes that colonize invasive grasses, thus giving an advantage to the invasives (Egerton-Warburton and Allen 2000, Siguenza et al. 2006). It is also possible that an increase in abundance of nonnative grasses in added-N plots could result in a positive feedback that further increases soil N level, due to higher N in grass litter than in native shrub litter (Wolkovich et al. 2010). In our study, the cover of nonnative grasses remained high through 2011 (the year with greatest ambient precipitation), but decreased in 2012, presumably due to lower precipitation in that year (Figs. 2 and 3). Grasses were able to achieve highest cover in water reduction plots in 2011, possibly due to a combination of open space due to low shrub recovery and the additional precipitation of a fairly wet year. In 2012, when all plots received less water, grass cover decreased even in those plots with open space (Figs. 2 and 3).

Could the combination of reduced water and increased nitrogen during fire recovery lead to type conversion?

The combination of drought and N addition following fire resulted in the lowest cover of native plants in the final year of the study and increased the cover of the



PLATE 1. One of the water-reduction plots, showing the structure used to exclude precipitation (in the “open” position). Note the relatively low shrub cover and high grass cover compared to the surrounding landscape. Photo credit: S. Kimball.

invasive grass, *Bromus madritensis*, especially in 2011. Although regions with high N deposition are correlated with type conversions (Talluto and Suding 2008), experiments adding N to mature CSS stands have not been able to produce such shifts (Vourlitis et al. 2009). Nitrogen addition was less important than precipitation in determining cover of nonnative grasses and California native forbs in a desert study, although a combination of N addition with high precipitation favored nonnative grasses (Rao and Allen 2010). We hypothesize that type conversion in CSS is primarily caused by N addition in combination with fire, drought, or other disturbance that provide European grasses with open space to colonize (Wood et al. 2006).

The strong effect of drought on shrub cover is somewhat surprising given the drought-tolerating and drought-avoiding adaptations of CSS shrubs (Harrison et al. 1971, Miller et al. 1983, Desouza et al. 1986, Cowling et al. 2005, Rundel 2007). Increased establishment and growth of grasses in postfire CSS is presumably due to the transient creation of open space and increased availability of light and other resources (Zedler et al. 1983, Keeley et al. 2005a). The degree to which nonnative grasses are able to persist may depend on the degree to which native shrubs recover after fire (Keeley et al. 2005a). Grass cover remains elevated if shrub cover fails to increase due to mortality or lack of germination or growth (Zedler et al. 1983, Keeley and Brennan 2012). Reduced water input limited the

recovery of shrubs in our study by reducing survival and growth of re-sprouts, and probably also by limiting recruitment following fire (Moreno et al. 2011). It is also possible that the nonnative grasses may have prevented shrub seedlings from becoming established in water reduction and added-N plots, since they maintained relatively high abundance in those treatments and have been found to competitively suppress native shrub seed germination and seedling growth (Eliason and Allen 1997).

One difficulty in assessing vegetation-type conversion is that there is no established definition, although it generally describes a shift in dominant vegetation type (Syphard et al. 2006, Talluto and Suding 2008, Ramirez et al. 2012). In one study, nonnative grassland was defined as having <20% cover of shrubs (Minnich and Dezzani 1998). It may be unclear whether a shift in percent cover is temporary or represents a new stable state (Suding and Hobbs 2009). Shrub cover was below 50% in the water reduction plots in 2011, while grass cover was greater than 50%, a pattern that might have been interpreted as a vegetation-type conversion. However, the next year was quite dry, and while shrub cover remained low (27%) in water reduction, added-N plots in 2012, grass cover also decreased to slightly less than the cover of shrubs (19% in reduced-water, added-N plots). This leads to an ambiguous result; a longer set of observations will be needed to determine whether water reduction plots experienced vegetation-type con-

version or if the plots represented areas with diminished or delayed shrub recovery that will not sustain high cover of grasses through time. Another important issue is whether the observed changes in species composition resist the termination of the water and nitrogen manipulations, in which case the manipulations would have caused a lasting decline in shrub density, or whether the decline in shrub cover is rapidly reversed by the resumption of ambient water and nitrogen input to all plots.

Our results indicate that CSS may be especially vulnerable to species shifts during the early stages of fire recovery. Fire and drought are increasing through time along with N deposition, making it likely that decreasing shrub cover facilitated by N will occur more frequently (Allen et al. 1998, Syphard et al. 2006). In this study, following fire, drought, and N addition, we observed decreased shrub cover compared to ambient conditions, highlighting that multiple global change stressors combine to threaten CSS and other mediterranean-climate shrublands (Klausmeyer and Shaw 2009).

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SUPPLEMENTAL MATERIAL

Appendix

Tables with full species names and results of statistical analyses, including repeated-measures ANOVA tables, Tukey post hoc comparisons, Pearson correlation coefficients of species with ordination space, analyses of shrub survivorship and growth, and PERMANOVA table on Bray-Curtis distances of community composition ([Ecological Archives A024-083-A1](#)).