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Seed banks of native forbs, but not exotic grasses, increase during extreme drought

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Abstract. Extreme droughts such as the one that affected California in 2012–2015 have been linked to severe ecological consequences in perennial-dominated communities such as forests. In annual communities, drought impacts are difficult to assess because many species persist through facultative multiyear seed dormancy, which leads to the development of seed banks. Impacts of extreme drought on the abundance and composition of the seed banks of whole communities are little known. In 80 heterogeneous grassland plots where cover is dominated by ~15 species of exotic annual grasses and diversity is dominated by ~70 species of native annual forbs, we grew out seeds from soil cores collected early in the California drought (2012) and later in the multiyear drought (2014), and analyzed drought-associated changes in the seed bank. Over the course of the study we identified more than 22,000 seedlings to species. We found that seeds of exotic annual grasses declined sharply in abundance during the drought while seeds of native annual forbs increased, a pattern that resembled but was even stronger than the changes in aboveground cover of these groups. Consistent with the expectation that low specific leaf area (SLA) is an indicator of drought tolerance, we found that the community-weighted mean SLA of annual forbs declined both in the seed bank and in the aboveground community, as low-SLA forbs increased disproportionately. In this system, seed dormancy reinforces the indirect benefits of extreme drought to the native forb community.

Key words: drought; exotic; extreme climate event; forb; functional trait; grass; grassland; native; seed bank; specific leaf area.

Introduction

Climate change is projected to increase both the frequency and severity of extreme events, including drought (Easterling et al. 2000, IPCC 2014, Swain et al. 2016). From 2012 to 2015, California experienced one of the most extreme droughts in the last 1,200 yr (Griffin and Anchukaitis 2014, Robeson 2015), causing widespread tree die-offs (Young et al. 2017) and lower agricultural output (Howitt et al. 2014). The effects of severe drought on annual plant communities, however, are less clear because many annual plants produce seeds with multiyear dormancy, leading to the formation of substantial and potentially long-lasting seed banks (Baskin and Baskin 2014). Previous research on drought impacts on annual communities has focused almost exclusively on aboveground life stages of plants and not directly measured abundances in seed banks. This research has identified some consistent community-level effects of drought: experimentally imposed drought led to the loss of shallow-rooted species (Kimball et al. 2016) while long-term observational data has similarly revealed the disproportionate loss of high specific leaf area (SLA; g/mm^2 dry mass) species under aridification (Harrison et al. 2010, 2015). Without taking seed banks into account, however, conclusions about drought impacts on community composition and diversity remain tentative, because observed loss of a species aboveground may not signal a loss of the species from the community. In this study, we quantify changes in annual plant seed banks during an extreme drought event and compare these to aboveground cover estimates to provide a fuller picture of a diverse annual plant community's response to drought.

Seed banks spread germination out over time to reduce the likelihood of large population declines during unfavorable periods (Baskin and Baskin 2014). This strategy is particularly beneficial in variable environments where lower climatic predictability leads to higher variability in mean growth rates (Ellner 1987). By keeping a portion of their seed dormant, seed banking species incur less of a cost during climatically bad years, such as a drought (Cohen 1966, Philippi 1993). Although seed banks strongly affect both the restoration potential and the resilience of a community (Hopfensperger 2007), we know very little about how communities dominated by seed banking species respond to severe drought events or even to climate change in general (Ooi 2012). An increase in drought frequency and severity could increase the probability of failed germination or of seedling mortality (Ooi 2012) while higher soil temperatures have been shown to increase germination in some species and lower seed viability in other species (Ooi et al. 2009), all of which could limit aboveground recovery of these systems after a disturbance.

Species with stronger facultative dormancy are thought to be generally less drought-tolerant once they germinate (Brown and Venable 1986), exhibiting lower water use efficiency and higher relative growth rates (Huxman et al. 2008, Huang et al. 2016). These species also typically have higher SLA, a trait associated with wetter climates (Westoby et al.

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2002) as well as wetter years (Kimball et al. 2012), while low SLA species with less persistent seed banks are more reliant on drought tolerant traits such as deeper roots and higher water use efficiency (Farooq et al. 2009). Therefore, high-SLA species that are disappearing aboveground may be remaining dormant belowground. Species without adaptive dormancy or drought-tolerant traits are likely to be highly sensitive to variability in climate and intense droughts.

Diversity in California annual grasslands is dominated by native annual forbs, many of which are known for undergoing multiyear seed dormancy. Many of these forbs have bet-hedging strategies, germinating only a portion of their seeds each year, and often delay their germination until the onset of cooler rains that are indicative of more reliable winter rainfall (Levine et al. 2008, Mayfield et al. 2014). The floral diversity in this region, however, is threatened by exotic annual grasses, which dominate the landscape in cover and biomass. This dominance is due in part to their extremely high annual seed production (as high as 60,000 seeds/m^2), their high relative growth rates that make them competitively superior to their native counterparts, and their buildup of thatch that also limits germination in native annuals (Bartolome 1979, D'Antonio et al. 2007). Instead of relying on persistent seed banks, these exotic annual grasses have shorter seed longevity and readily germinate a larger proportion of their annual seed each year (Thompson and Grime 1979, Jain 1982).

We analyzed drought-induced changes in the seed bank by growing out seeds from two sets of soil cores collected in fall 2012 and fall 2014 in a northern California grassland. A previous study at the same site found that the extreme 2012–2014 drought caused aboveground cover of exotic annual grasses, but not native forbs, to decline even more than expected based on community responses to normal interannual variability (Copeland et al. 2016). Long-term work at this site also showed that dry years cause high-SLA forbs to decline in aboveground cover and diversity relative to low-SLA forbs (Harrison et al. 2015, 2017). Thus, based simply on changes in aboveground abundance and seed input, we predicted that (1) abundance of exotic annual grass seeds in the seed bank would decline more during the severe drought than the abundance of native annual forb seeds, and (2) high-SLA native annual forbs would decline more in the seed bank than low-SLA forbs, leading to lower community weighted mean SLA of native annual forbs in the seed bank in 2014 than 2012. In addition, higher drought-induced dormancy in forbs than grasses should tend to strengthen prediction (1), while higher drought-induced dormancy in high-SLA than low-SLA forbs should tend to weaken prediction (2); to evaluate these possibilities, we compared changes in seed bank composition to the corresponding changes in aboveground cover of these functional groups.

METHODS

Collection site and greenhouse study

This study took place in a heterogeneous, annual-dominated grassland at University of California McLaughlin Natural Reserve (https://naturalreserves.ucdavis.edu/mclaughlin-reserve) in the Inner North Coast Range (N 38°52′, W 122°26′). The site has a Mediterranean climate with cool wet winters and dry hot summers; pre-drought annual winter precipitation averaged 46.4 cm (1981–2011) and winter mean temperatures averaged 7.9°C (Flint and Flint 2014). During the recent extreme drought (2012–2014), winter precipitation at our site averaged 26.6 cm and winter mean temperature averaged 9.3°C. Annual plants in this community germinate in fall (September–December) shortly after rains begin, are present as seedlings during winter (December–February), and flower in spring (March–May) or summer (June–September).

Our study used a set of 80 vegetation-monitoring plots that were chosen haphazardly and are widely dispersed across the reserve; 42 are on fertile soils derived from volcanic and sedimentary rocks and are dominated by exotic annual grasses, while 38 are on infertile soils derived from serpentine rock and have substantially higher native diversity (mean of 17 species per 5-m^2 in serpentine soils vs. a mean of 9 per 5-m^2 on non-serpentine soils). Each plot consists of five permanently marked 1-m^2 subplots along a 40-m transect where visual estimates of species cover ("aboveground data") were recorded twice annually in April and June to capture peak cover for both early- and late-flowering species. See Harrison (1999), Elmendorf and Harrison (2009), Fernandez-Going et al. (2012), and Harrison et al. (2017) for further details and previous analyses of aboveground data from these plots. All vegetation surveys used in the present study were done using a 1-m^2 sampling frame and were carried out by the same trained and experienced person with a minimum estimate threshold of 0.1%. Here we chose to focus our analysis on two functional groups: exotic annual grasses, which form >90% of the cover and are well known to be the dominant competitors in Californian grasslands (Eviner 2016), and native annual forbs, which comprise 44.5% of the species diversity in our sites and are the focus of considerable ecological and conservation interest (Eviner 2016).

In 2012, early in the drought, and again in 2014, late in the drought, we collected five soil cores per plot (one from each subplot) and aggregated the cores into one sample per plot, giving us a total of 80 samples in each year. Soil cores were 5 cm in diameter and were taken from the top 10 cm of soil. Samples were collected in September of each year in question, after seeds from the previous growing season had set but before germination for the next growing season began.

We sifted the samples to remove rocks and large vegetation fragments. After samples were homogenized, we mixed a 1 kg subsample with equal parts sand to improve drainage due to the high clay content of soils from the site. We then spread out each sample in half flats (10.875 inches wide × 10.875 inches long × 2.25 inches deep) and placed the flats in a shade house in the UC Davis Greenhouse Complex where they were open to the natural background temperature variation. Flats were watered daily throughout the growing season, stirred before drying down for the summer, then resumed watering for another growing season. Every seedling that emerged was identified to species, recorded, and discarded ("belowground data"). In total, we recorded just over 11,000 seedlings during each year of the study from a total of 126 annual species.

Specific leaf area

We focused on SLA because of its known correlation with both water use efficiency (WUE) and relative growth rate (RGR; Reich et al. 1999, Wright et al. 2004). Specific leaf area (SLA) was measured in 2010 on 10 individuals per species (Spasojevic et al. 2012) following standard protocols (Cornelissen et al. 2003). To determine the average SLA of a community, we calculated community weighted mean SLA for each plot which weights the SLA contribution of a particular species to the mean SLA by its relative abundance in the community (Garnier et al. 2004).

Data analysis

To test for stronger declines in seed bank abundances of grasses than seed banks of forbs (prediction 1), we used generalized linear mixed effects models with number of seeds summed by functional group as the response variable, and year, functional group (native forb or exotic grass), and their interaction as the predictor variables, and a random slope for functional group nested within each plot. Seed counts were modeled using a negative binomial regression model because count data were overdispersed.

To compare the aboveground changes to the seed bank results for Prediction 1, we conducted similar analyses on cover data. We used a linear mixed effects model on square root-transformed cover values also summed by functional group with year, functional group, and their interaction as the predictor variables, and a random slope for functional group within each plot. For both analyses, we conducted multiple comparison tests using the glht function in the multcomp library (Hothorn et al. 2008) to compare seed bank abundances and cover across years. We adjusted *P*-values using Benjamini–Hochberg corrections to account for multiple comparisons (Benjamini and Hochberg 1995).

To test for declines in community weighted SLA of forbs (prediction 2), we used a linear mixed effect model on log-transformed community weighted SLA data with year and community type (seed bank or aboveground), and their interactions as the predictor variables, and a random slope for community type within each plot. We then analyzed changes in belowground abundance of species with high vs. low SLA to test whether these changes were driven by low- or high-SLA species. Species with below-median SLA for a given plot were classified as low SLA species, while those with above-median SLA for a given plot were classified as high SLA species. We then ran a negative binomial regression model on summed seed bank abundance at the plot level with year, high vs. low SLA, and their interaction as predictor variables, and a random slope for high vs. low SLA species nested within each plot. For aboveground data, we used a linear mixed effects model on square root-transformed cover data, also summed by SLA group, again with year, high vs. low SLA, and their interaction as predictor variables, and a random slope for high vs. low SLA species nested within each plot. We then conducted multiple comparison tests using the glht function in the multcomp library (Hothorn et al. 2008) to compare SLA changes across years. We adjusted *P*-values using Benjamini–Hochberg corrections to account for multiple comparisons (Benjamini and Hochberg 1995).

Due to the different species composition of grasslands on serpentine and non-serpentine soils, we also ran all models including soil type as a predictor as well as its interaction with other predictors. Although there were significant quantitative differences in abundance, cover, and community weighted SLA changes between soil types, the directional change of all our variables did not vary by soil type and thus inclusion of soil type did not qualitatively change the results (Appendix S1: Tables S1, S2 and Figs. S1–S3). All data analyses were done in R version 3.3.1 (R Core Team 2016).

Results

Seed bank abundance

In agreement with Prediction 1, we found that seed abundance belowground of exotic annual grasses significantly declined from 2012 to 2014 ($Z = -7.76$, $P < 0.001$; Fig. 1a) while native annual forbs significantly increased over the course of the drought ($Z = 9.61$, $P < 0.001$; Fig. 1a). To determine whether the observed community-level changes were driven by many or only a few species, we tabulated the direction of change for each species. We found that the trends were generally consistent across species. In the seed bank, 11 of 15 grass species declined in seed bank abundance, while only 4 grass species increased in abundance (Fig. 2; Appendix S1: Table S3). In contrast, 65 of 81 native annual forb species increased in abundance in the seed bank, while only 14 species declined in abundance and 2 species displayed no change (Fig. 2; Appendix S1: Table S3).

Specific leaf area

In partial agreement with Prediction 2, community weighted mean SLA of the forb community decreased significantly in the seed bank from 2012 to 2014 ($Z = -1.99$, $P = 0.05$; Fig. 4). However, rather than being driven by a decrease in high-SLA forbs as predicted, this pattern was driven by a large increase in seeds of low-SLA forbs. Although both forb species with below-median SLA and forbs with above-median SLA for a given plot significantly increased in summed abundance (Table 1), below-median SLA species increased by 263% while above-median SLA species increased by 119%.

Aboveground comparisons

Aboveground, we found that grass cover significantly decreased ($Z = -6.95$, $P < 0.001$; Fig. 1b) while forb cover significantly increased ($Z = 2.63$, $P = 0.01$; Fig. 1b). These changes were smaller in magnitude than the corresponding changes in the seed bank (grasses: −39% aboveground vs. −52% in seed bank; forbs: +14% aboveground vs. +201% in seed bank). As we did for seed bank abundance, we compared these functional group level contrasts to trends in cover of individual species. Aboveground, 11 of 14 grass species declined in cover, while only 3 grass species increased (Fig. 3; Appendix S1: Table S3). In contrast, 52 of 88 native forb species increased in cover, while 35 decreased and 1 species displayed no change (Fig. 3; Appendix S1: Table S3).

Community weighted mean SLA also significantly decreased aboveground ($Z = -2.03$, $P = 0.05$; Fig. 4). Similar to the

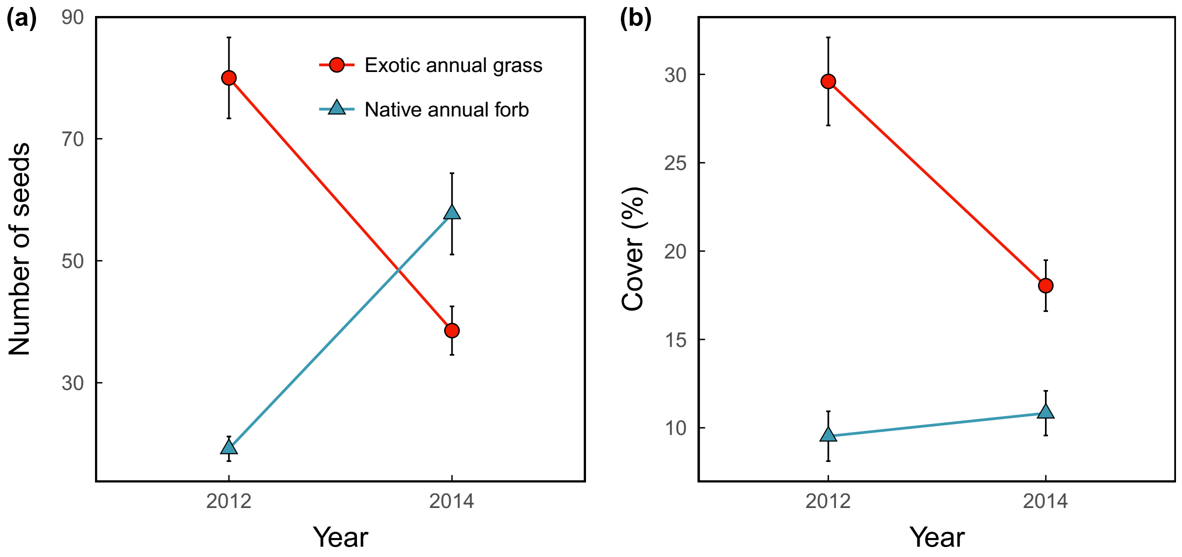

FIG. 1. (a) Seed bank abundance and (b) percent cover of grasses (circles; N = 80) and forbs (triangles; N = 80) in 2012 and 2014. Error bars show standard error at the plot level.

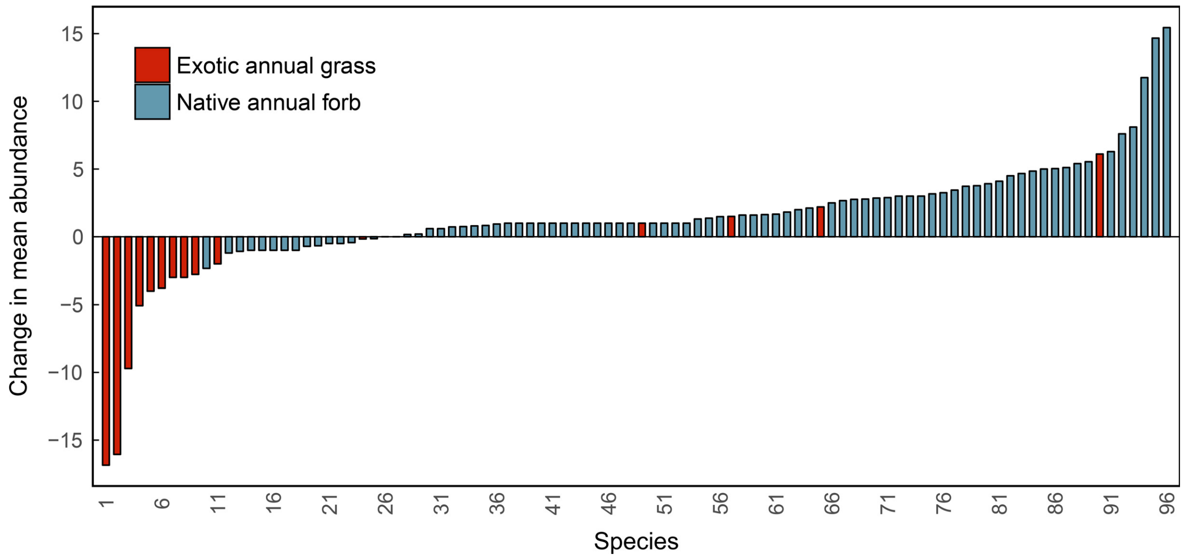

FIG. 2. Mean change in seed bank abundance per species (15 exotic annual grass species and 81 native annual forb species). See Appendix S1: Table S3 for a list of species and their associated changes in abundance.

TABLE 1. Means and standard errors (SE) of above- and below-median SLA species in the seed bank (count) and aboveground (cover) in 2012 and 2014 along with model contrasts.

	2012		2014				
Category and variable	Mean	SE	Mean	SE	*Z*	*P*	Change (%)
Above-median SLA species							
Seed bank abundance	7.97	0.96	17.45	2.83	4.46	**<0.001**	119.0
Aboveground cover	4.26	0.84	2.80	0.44	−1.40	0.16	−34.3
Below-median SLA species							
Seed bank abundance	8.43	1.13	30.59	4.32	9.78	**<0.001**	263.0
Aboveground cover	6.51	0.95	7.36	0.97	2.57	**0.02**	13.1

Note: Bolded values indicate a significance level of $P \leq 0.05$.

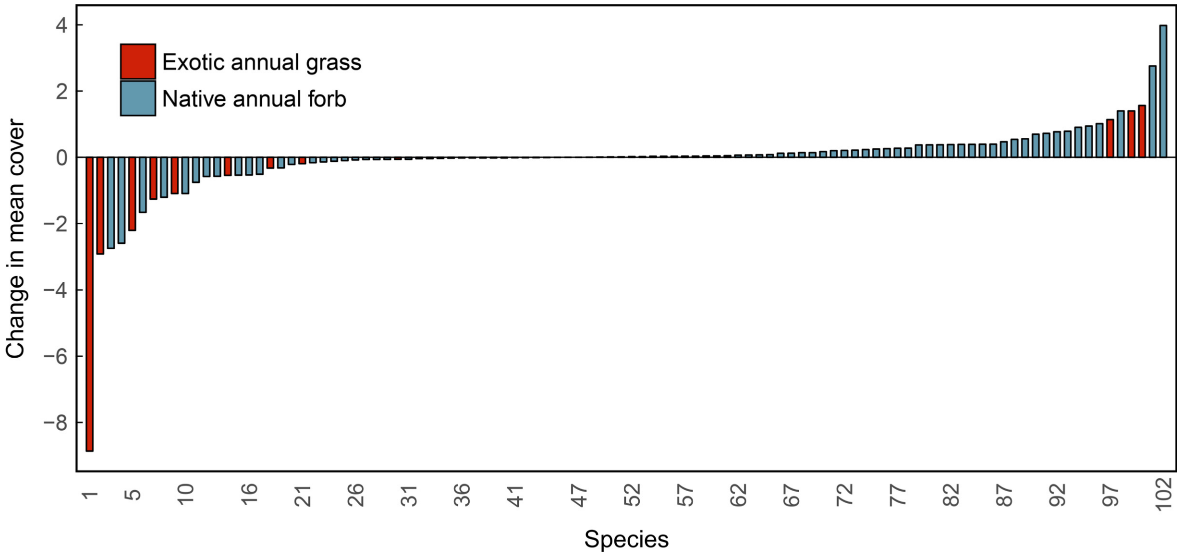

FIG. 3. Mean change in percent cover per species (14 exotic annual grass species and 88 native annual forb species). See Appendix S1: Table S3 for a list of species and their associated changes in cover.

change in the seed bank, this change was driven by an increase in low-SLA forbs; summed cover of species with below-median SLA significantly increased by 13%, while summed cover of those with above-median SLA decreased non-significantly (Table 1). Community weighted mean SLA was higher for the seed bank than for the aboveground community in both years (2012: 20% higher, $P < 0.001$; 2014: 21% higher, $P < 0.001$).

DISCUSSION

Together, our results reveal that the grass and forb abundance changed in the same direction both above- and belowground in response to drought, but that the magnitude of each functional group's response was stronger belowground. Moreover, these changes were well predicted by both the drought tolerances and seed dormancy tendencies of the different functional groups. Exotic annual grasses suffered the strongest negative effects with a 52% decline in belowground seed bank abundance between 2012 and 2014. This belowground decline mirrored their 39% decline in aboveground cover, a decline that significantly exceeded the drought response predicted from normal interannual variability (Copeland et al. 2016). Our work supports other studies on annual grasses that found a large decrease in grass seed banks during an experimentally imposed drought (Hild et al. 2001), as well as negative aboveground responses to decreased rainfall including increased senescence and mortality (Clary et al. 2004), reduced competitive effects (Sheley and James 2014), and decreased densities (Salo 2004). While the observed decline in grass abundances may have resulted from decreased germination, survival (either in the seed or post-germination stage), growth, and/or seed production throughout the drought, the even stronger decreased abundance of seeds attests to a low capacity for population-level buffering through facultative seed dormancy, also in accord with work in other arid, annual-grass invaded systems (Forcella and Gill 1986, Harel et al. 2011).

In contrast to grasses, native forbs significantly increased in both seed bank abundance and aboveground cover during the drought. The 201% increase in native forb seed bank abundance was considerably larger than the 14% increase in cover aboveground, suggesting that the drought induced much higher levels of seed dormancy in these species, especially the high-SLA forbs, which did not increase in abundance aboveground. Our results also suggest that the enlarged native annual forb seed bank during the drought was mainly driven by the low-SLA, drought-tolerant species, which increased in abundance belowground and in cover aboveground in contrast to the drought-intolerant high-SLA species, which displayed a smaller yet still sizeable increase

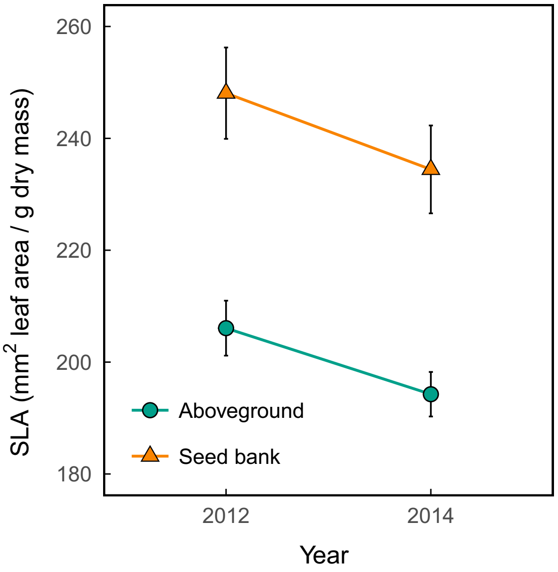

FIG. 4. Community weighted mean specific leaf area of native annual forbs in 2012 and 2014 calculated using cover aboveground (circles) and abundance in the seed bank (triangles). Error bars show standard error at the plot level.

in abundance belowground and a non-significant decrease aboveground. Similar patterns of increased dormancy during dry years have also been observed in desert annual plants (Pake and Venable 1996, Venable 2007, Angert et al. 2009).

The evident benefit of the drought to the native annual forb community both below- and aboveground is consistent with theoretical (Levine and Rees 2004) and previous empirical evidence (Suttle et al. 2007, Dudney et al. 2017) pointing to the positive effects of reduced competition from exotic annual grasses. However, some other studies have found the direct negative effects of droughts on native annual diversity to outweigh the positive indirect ones (Tilman and Haddi 1992, Pfeifer-Meister et al. 2016). One possible explanation of this discrepancy is that our site underwent a longer-term trend toward drier winters during the 12 yr preceding the drought, which was associated with trends toward lower forb diversity and a lesser prevalence of drought-intolerant species (Harrison et al. 2015). Thus, the communities we studied may have already been disproportionately poor in drought-intolerant species by 2012.

Our findings also support other work that showed that mesic-adapted species maintain larger proportions of their populations in a dormant state in the seed bank than species that are better equipped to tolerate drought stress once germinated (Brown and Venable 1986). The seed bank, acting as a reservoir for the less drought-tolerant forbs, had a significantly higher weighted SLA across years compared to aboveground communities. We have already seen similar trends in interannual variability in our system, where local species richness is higher in wet years, with only a nested, smaller subset of species appearing in drier, hotter years (Elmendorf and Harrison 2009, Fernandez-Going et al. 2012). Similarly, extensive work in desert annual systems has found that stress-tolerant plants with higher water use efficiency and lower relative growth rates have more buffered population dynamics and higher germination fractions while species with lower water use efficiency and higher relative growth rates had more variable survival and fecundity and much lower germination fractions, indicating a higher tendency for seed banking in these species (Pake and Venable 1996, Angert et al. 2007, Venable 2007, Huxman et al. 2008, Huang et al. 2016).

The exotic annual grasses that currently dominate Californian grasslands are found in disturbed environments in their native range in the Mediterranean basin (Jackson 1985). They evolved to be highly ruderal and flexible, with high relative growth rates, high reproductive effort, and rapid germination allowing them to increase rapidly in wet years (Jackson 1985, Salo 2004). Such a high-risk, high-reward strategy becomes less advantageous as the probability of a wet winter decreases (Ellner 1987). Since their introduction to California in the mid- to late-1800s (D'Antonio et al. 2007), there have been no years nearly as dry as 2014 (Griffin and Anchukaitis 2014). The cumulative 3-yr (2012–2014) Palmer Drought Severity Index of −14.55 was the worst drought on record, even more extreme than longer (4–9 yr) droughts (Griffin and Anchukaitis 2014), indicating that the grasses have not yet been exposed to a drought of this severity. With such an extreme response in the annual grass community, there would likely be a lag before grass populations recover even with a return to wetter, more favorable conditions. Since these grasses play critical ecosystem roles, including as competitors with native plants (Barger et al. 2003), forage for livestock (Huntsinger et al. 2007), cover for wildlife (Schiffman 2007), food resources for granivores (Schiffman 2007), and fuel for wildfires (D'Antonio and Vitousek 1992), prolonged droughts could have many cascading ecosystem consequences mediated by declines in annual grass abundance.

While these results may give a positive outlook for native annual forb populations under drought, it is likely perennial bunchgrasses that have been similarly affected by exotic annual grass invasion in California will not be as resilient to increased drought. Perennial bunchgrasses are better adapted to wetter climates and occur in higher abundances along the coast of California and in areas with higher summer rainfall and lower variation in temperature and rainfall (Clary 2012). These bunchgrasses also tend to be competition and disturbance intolerant (Dyer and Rice 1999, Maron and Marler 2008) and to lack a persistent seed bank (Hild et al. 2001, Gibson 2009). The best recovery targets for California's grasslands may therefore be increased populations of native forbs, rather than native bunchgrasses.

Overall, our results highlight the dramatic negative effect of severe droughts on annual grass dominance in this system, and an unexpected neutral-to-positive response in competitively inferior native forbs. Underlying this response was facultative seed dormancy in the drought-intolerant competitively inferior natives, combined with a release from grass competition that benefited the aboveground success of drought-tolerant, low-SLA native annual forbs. The drought-intolerant native forbs appear resilient to a single extreme drought event; however, it is possible that more frequent severe or prolonged future droughts could eventually exceed the adaptive capacity of native species to survive through seed dormancy.

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