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Lagging behind: have we overlooked previous-year rainfall effects in annual grasslands?

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Summary

1. Rainfall is a key determinant of production and composition in arid and semi-arid systems. Long-term studies relating composition and water availability primarily focus on current-year precipitation patterns, though mounting evidence highlights the importance of previous-year rainfall particularly in grasslands dominated by perennial species. The extent to which lagged precipitation effects occur in annual grasslands, however, remains largely unexplored.

2. We pair a long-term study with two manipulative experiments to identify patterns and mechanisms of lagged precipitation effects in annual grasslands. The long-term study captured variation in functional group (exotic annual forbs and grasses) abundance and precipitation across 8 years at three northern California grassland sites. We then tested whether lagged rainfall effects were created through seed production and litter (residual dry matter, RDM) by manipulating rainfall and litter, respectively.

3. Rainfall from the previous-year growing season (both seasonal and total rainfall) shifted functional group abundance. High lagged rainfall was associated with increased grass and decreased forb abundance the following year. Current-year seasonal rainfall also influenced species composition, with winter rain increasing forb and decreasing grass abundance. Lagged precipitation effects were generally stronger for forbs than for grasses. Our experimental studies provided evidence for two mechanisms that contributed to lagged effects in annual grasslands. Higher rainfall increased seed production for grasses, which translated to more germinable seed the following year. Higher rainfall also increased biomass production and RDM, which benefited grasses and reduced forb abundance.

4. *Synthesis*. Our results highlight the importance of previous-year precipitation in structuring annual community composition and suggest two important biotic pathways, seed rain and RDM, that regulate lagged community responses to rainfall. Incorporating lagged effects into models of grassland diversity and productivity could improve predictions of climate change impacts in annual grasslands.

Key-words: annual plant seed production, determinants of plant community diversity and structure, functional groups, lagged effects, legacy effects, litter dynamics, plant population and community dynamics, plant–climate interactions, precipitation effects, species responses to weather

Introduction

Describing how resource availability modifies ecosystem structure is a long-standing ecological challenge and increasingly more important given the uncertainties surrounding climate change. Water availability is a strong driver of plant community structure in a number of systems (Noy-Meir 1973; Westoby, Walker & Noy-Meir 1989) and can lead to shifts in species diversity and composition over time (Cleland *et al.* 2013). Rainfall-driven fluctuations in composition are particularly pronounced in annual grasslands. For example, wet years often promote recruitment of all species, while only

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*Correspondence author. E-mail: jdudney@berkeley.edu a subset of species survive in dry years (Cleland *et al.* 2013). In addition, different life-history strategies may generate trade-offs between species in response to rainfall patterns (Pitt & Heady 1978; Huenneke *et al.* 2002; Robertson, Zak & Tissue 2010), yielding rainfall-induced species shifts across years.

Mounting evidence indicates that previous-year rainfall (i.e. a lagged effect) also drives community composition (Gibbens & Beck 1988; Dunnett *et al.* 1998; Adler & Levine 2007; Sherry *et al.* 2012). Lagged effects have been investigated almost exclusively in mixed perennial grasslands, though Hobbs & Mooney (1995) demonstrated a significant previous-year rainfall effect on the native forb, *Lasthenia californica* (Lindl.) in serpentine soils. Lagged effects can explain a significant portion of the unexplained variance in models with current-year precipitation and production (Sherry *et al.* 2008; Reichmann, Sala & Peters 2012). Lagged rainfall shifts dominance hierarchies among species (Sherry *et al.* 2012) and modifies competitive advantages with consecutive dry or wet conditions (Dunnett *et al.* 1998). A variety of mechanisms, including precipitation-driven changes in plant reproduction and litter dynamics (Herben *et al.* 1995; Sherry *et al.* 2008), help explain these lagged effects. Here, we extend this research to consider broader patterns and mechanisms of lagged effects in annual-dominated communities.

Previous-year rainfall could impact annual community composition the following year by altering seed production (Hobbs & Mooney 1995). Because many grass species rely on transient seedbanks (i.e. seed from the previous year) (Bartolome 1979; Seabloom *et al.* 2003), their growth is highly dependent on conditions that influence seed production (Chippendale & Milton; Major & Pyott 1966). Other species with persistent seedbanks (Peco, Espigares & Levassor 1998; Scott & Morgan 2012) may exhibit minimal lagged effects, as their seeds can accumulate across multiple years. Longer seed viability enables these species (e.g. various forbs) to wait until growing conditions are more favourable (Levine, Rees & Bolker 2004) and reduces their dependence on previous-year seed rain. Thus, different seed banking strategies, combined with previous-year seed production, could create lagged effects on species composition in annual-dominated systems.

Lagged effects may also occur if biomass production from the previous year produces litter that modifies microsite availability in the current year. In annual grasslands, precipitation has a strong control on community productivity and the litter remaining at the end of the season (Bartolome *et al.* 2002). Litter can modify the germination environment the following year by shading microsites and increasing nutrient deposition (Bartolome, Stroud & Heady 1980; Foster & Gross 1998). In fact, accumulation of litter in annual grasslands decreases forb richness and perpetuates dominance of high biomass-producing species (Hobbs & Mooney 1995; Huenneke *et al.* 2002; Bartolome *et al.* 2007b; Suttle, Thomsen & Power 2007). Thus, the interplay among rainfall, biomass production, microsite conditions and species recruitment produce complex effects on species composition that warrant further study.

Here, we evaluate whether previous-year annual and seasonal precipitation is a significant determinant of community composition in annual-dominated grasslands. Using three long-term species composition records from California, we observe how historical rainfall relates to functional group abundance. California's annual-dominated grasslands are an ideal system, as they are characterized by high precipitation variability (Potts *et al.* 2012) and strong rainfall effects (Pitt & Heady 1978; Hobbs & Mooney 1991; Jackson & Bartolome 2002; Zavaleta *et al.* 2003). We then experimentally isolate two potential mechanisms of lagged precipitation effects. We hypothesize: (i) differences in seed production between functional groups is directly related to precipitation and (ii) litter (residual dry matter, RDM) shifts species composition the following year (Fig. 1a–c).

Materials and methods

SYSTEM

We conducted the observational study and associated manipulative experiments in northern California valley grasslands within the California Ecological Province (Bartolome *et al.* 2007a). We collected abundance data at three sites in the East Bay Regional Park District, USA (37° N, 121° W): Vasco Caves Regional Preserve, Pleasanton Ridge Regional Park and Sunol Regional Wilderness. Manipulative experiments were difficult to conduct in the East Bay Parks due to open space regulations and high human and other animal traffic. Thus, we based experiments in a valley grassland at the University of California Sierra Foothill Research Extension Centre (SFREC), located in Browns Valley, California, USA (39°15′ N, 121°17′ W). Valley grasslands at SFREC and East Bay Parks are dominated by non-native annual species with patches of remnant natives. The most abundant species included *Avena fatua* Link, *Avena barbata* L., *Festuca perennis* L., *Bromus hordeaceus* L., *Erodium botrys* (Cav.) *Bertol.* and *Erodium cicutarium* (L.) *Aiton* (nomenclature follows Baldwin *et al.* 2012; see Appendix S1 in Supporting Information). Based on species composition and average annual rainfall, both sites fall within the annual grassland/hardwood range (Bartolome *et al.* 2002). Grasslands at both locales are characterized by having silty and clay loamy soils (Dahlgren *et al.* 2003; Gea-Izquierdo, Gennet & Bartolome 2007). Because of the similarities in vegetation type, soils and climate, we expect parallel responses to precipitation between both research sites.

DETECTING A PATTERN OF LAGGED PRECIPITATION EFFECTS

Sampling design

Between 2005 and 2012, we sampled 18 permanent plots (six plots in each of the three East Bay Parks). Permanent plots were established in 2003 using a stratified random sampling design, which ensured plot placement at least 300 m from non-grassland vegetation (e.g. oak woodland, chaparral) (Spiegal *et al.* 2014). Returning researchers trained the new field assistants in species identification techniques to maintain consistency throughout years. Species composition was measured at peak biomass between April and May, depending on rainfall conditions. Four, 17-m transects were arrayed in the cardinal directions from the centre of each *c.* 900 m^2 circular plot (Heady, Gibbens

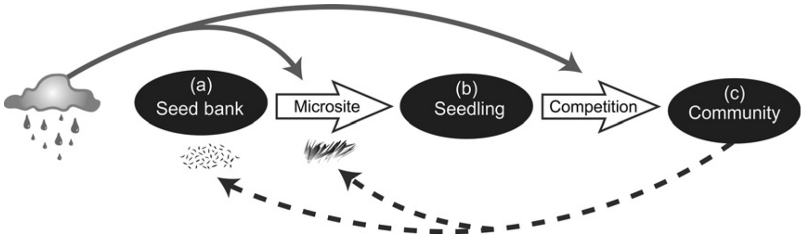

Fig. 1. Conceptual diagram of lagged effects in annual-dominated grasslands (i.e. the carry-over effects of vegetation from the previous year on current year's species composition). (a) Species germination is mediated by the magnitude of rainfall, seed bank dynamics and microsite availability. (b) Species that germinate grow and compete; their growth and competitive interactions are constrained by the magnitude of rainfall throughout the growing season (fall, winter and spring). (c) Seed production and peak biomass from the resulting community become the biotic feedbacks that modify the seed bank and microsite availability the following year.

& Powell 1959). Using a small diameter, metal pole placed perpendicular to the transect line, either first-hit species, litter or bare ground was recorded 70 times along each of the four transects, for a total of 280 individual records per plot (Spiegal & Wenk 2009). Species abundance was determined by counting the number of individuals identified in each plot. We did not relativize species abundances to avoid artificially inducing covariance among species (Hallett *et al.* 2014). All plots within the East Bay Parks were lightly cattle or sheep grazed throughout the study period.

Functional group classification

We classified the 80 different species sampled in our plots into six functional groups: exotic annual grasses, exotic annual forbs, exotic perennial forbs, native annual forbs, native perennial forbs and native perennial grasses. These functional groups were similar to previous classifications in California grasslands (Sandel *et al.* 2010; Fernandez-Going, Anacker & Harrison 2012) and based on the Jepson Manual, the standard flora for California (Baldwin *et al.* 2012).

Precipitation data

Precipitation data were downloaded from three different weather stations within the California Irrigation Management Information System (www.cimis.water.ca.gov/). All stations were located within 20 miles of each sampling site. We used Station 47 records with abundance data collected at Vasco Caves, Station 191 for Pleasanton Ridge and Station 171 for Sunol Regional Wilderness. Rainfall variables were calculated based on the local growing season, starting October 1 and ending May 31. We omitted the summer season (June–September) from our analysis, as previous research indicated these months do not significantly impact the vast majority of exotic annual species in our data set (Pitt & Heady 1978, p. 19). All but one of the exotic annual grasses (*Elymus caput-medusae*) and all but two of the exotic annual forbs (*Centaurea melitensis* and *Centaurea solstitialis*) in our data set were either at peak biomass or senescing during the time we sampled. *Centaurea* spp. and *Elymus caput-medusae*, however, are invasive species that produce the bulk of their biomass during late/early summer (Thomsen *et al.* 1996). Consequently, their dynamics are affected by summer precipitation (Chiariello 1989) and our results are more relevant for grasslands that are not heavily invaded by these species.

For our seasonal analyses, we summed precipitation across the following months: fall (October–November), winter (December–February) and spring (March–May). Because Station 191 did not have daily precipitation records before 2005, we regressed Station 191 with Station 171 weather variables and used the intercepts and estimates (P-value < 0.001) to derive precipitation for 2004. For all our precipitation data, lagged rainfall was simply the precipitation that fell the previous year. Lagged precipitation variables spanned the years 2004–2011 and current precipitation variables spanned the years 2005–2012. We scaled rainfall variables across years and within season (fall, winter and spring) at each site to ensure that fall and spring variability was not masked when compared against higher winter rainfall.

Over the study period, mean current-year, growing season rainfall was 378 mm (CV 0.36), while mean, previous-year rainfall was 391 mm (CV 0.33). On average, the majority of precipitation fell during the winter months, December–February (54%), about a third fell during the spring months, March–May (30%) and only 16% fell in fall, October–November. The magnitude of seasonal precipitation also fluctuated across growing seasons. For example, a wet winter was followed by a dry spring in 2008 (Fig. 2).

Statistical analysis

Using a general linear mixed model analysis with R software (R Core Team 2015), we tested how current and previous-year precipitation altered functional group abundances over 8 years. Since our count data were overdispersed (variance was greater than the mean), it was likely that using a Poisson model would inaccurately estimate the significance of the relationships between precipitation and abundance (Hilbe 2011). To account for the overdispersion, we used the negative binomial maximum likelihood (ML) method, which considers the mean as a random variable and assumes the extra variance is a quadratic function of the mean (Lindén & Mäntyniemi 2011). By using the negative binomial model, we could accept the significance of the independent variables with greater confidence (Zuur *et al.* 2009; Hilbe 2011).

To test for possible correlations among weather variables, we used Kendall's tau correlation matrix (Kendall 1948). None of the seasonal precipitation variables were significantly correlated above absolute value 0.3 (Robertson *et al.* 2009); however, annual precipitation was highly correlated with seasonal precipitation (see Table S1). To avoid confounding regression results, we created two sets of models for annual and seasonal precipitation parameters.

We fit six models using the function glmer.nb() from R package LME4 (Bates *et al.* 2015) for each of the functional groups to determine current and previous rainfall effects: (i) functional group abundance with current-year annual precipitation, (ii) functional group abundance with previous-year annual precipitation, (iii) functional group abundance with both current and lagged annual precipitation, (iv) functional group abundance with current-year seasonal (fall,

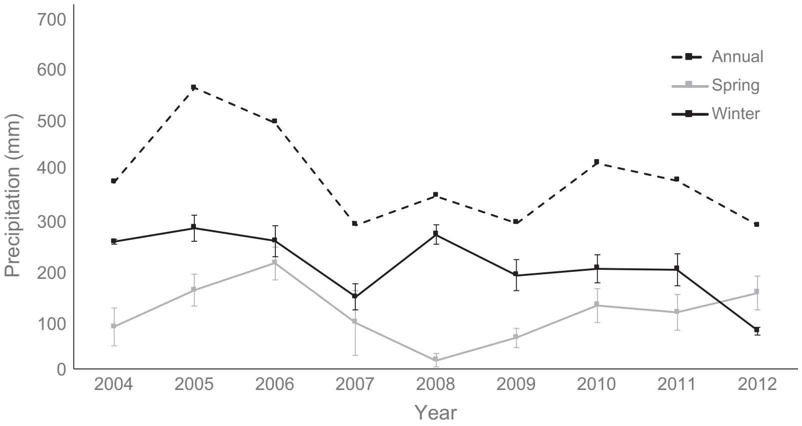

Fig. 2. Average growing season (October–May), spring (March–May) and winter (December–February) precipitation across 9 years. Averaged across the three weather stations. All points displaying standard deviation.

winter and spring) precipitation, (v) functional group abundance with previous-year seasonal precipitation and (vi) functional group abundance with current and lagged seasonal precipitation. We conducted our analyses at the plot level and accounted for the site-level variation among the three East Bay Parks and among all plots by including a nested random effects term in all our models (plot nested within site). To determine which model best explained abundance patterns, we used Akaike information criterion (AIC) to compare across all six models. Due to the exceptionally low abundances and high temporal variability (see Table S2) of the three native functional groups (native annual forbs, native annual grasses and native perennial forbs), we focused only on exotic annual forbs and grasses (Onwuegbuzie & Daniel 1999; Case & Ambrosius 2007).

TESTING POSSIBLE MECHANISMS OF LAGGED EFFECTS IN ANNUAL SYSTEMS

We tested two likely mechanisms of lagged precipitation effects: (i) an effect of RDM on current-year species composition and (ii) a differential effect of rainfall on species seed production, which should influence composition the following year. We implemented our experiments in two pastures at SFREC that were previously grazed by cattle but were fenced prior to our study to allow controlled manipulations.

Mechanism 1: Residual dry matter and species composition

Residual dry matter is the result of biomass production (associated with rainfall) and biomass removal (e.g. via grazing) (Bartolome *et al.* 2007b). Biomass removal was the most feasible way to manipulate RDM in the field. Therefore, we tested the effect of RDM on species composition using a mowing/trampling experiment. We used a combination of trampling by livestock and mechanical mowing treatments to establish a gradient of six RDM levels. Our lowest RDM level corresponded closely with the stocking rate regulations at the East Bay Parks, which stipulate that RDM must not fall below 112 g m^{-2} (www.ebparks.org/about/stewardship/grazing). Our highest RDM level (no biomass removal) corresponded roughly with the maximum potential RDM at the Parks, which have similar species composition but lower average rainfall than SFREC. Thus, the RDM manipulations at SFREC were likely within the range of RDM variation at the East Bay Parks, as well as other studies that manipulated RDM (Bartolome *et al.* 2007b; Amatangelo, Dukes & Field 2008).

The RDM treatments were replicated four times in two pastures for a total of eight 10 × 3 m replicate blocks per level (described by Stein *et al.* 2014). The gradient was created as follows: (i) not trampled or mowed; (ii) trampled once per year, in late March when plants started flowering; (iii) trampled twice per year, in late March and in June/July after most plants were senescent; (iv) an additional mowing right before the late March trampling treatment; (v) mowing prior to each trampling treatment; and (vi) an additional mowing in late February during early plant growth. We repeated this experiment over four growing seasons (2008–2011).

We harvested RDM in early October each year by clipping a 0.25 × 0.25 m subplot within each replicate, drying the biomass (60 °C for 72 h) and weighing it. To avoid re-harvesting the same area, we shifted the subplot position each year. We verified that our mowing/trampling treatments resulted in an RDM gradient using a linear mixed effect model with RDM level and year as fixed factors, and plot nested in block nested in pasture as random effects. Analyses were conducted using the lme function in the NLME package in R (Bates *et al.* 2015).

We visually estimated species cover (cover classes included: 1, 2, 5, 10, 20, 30… up to 100% cover per species) in a 1 × 1 m subplot within every replicate in mid-April of each year. Total species cover could be >100, owing to canopy overlap or <100, owing to bare ground. We aggregated the cover of annual grass and annual forb species separately and analysed their responses to the RDM gradient using a linear mixed effect model with cover as the response variable. Fixed factors included functional group (grass, forb), RDM level, year and functional group × RDM level. Random effects comprised plot nested in block nested in pasture. An effect in which grass cover increased with RDM while forb cover decreased would support RDM accumulation as a mechanism of lagged precipitation effects on functional group abundance.

Mechanism 2: Seed production and rainfall variation

To test whether rainfall shifted seed production, we manipulated rainfall using rainout shelters and irrigation to create dry and wet conditions over the course of the 2012 growing season. Each dry/wet pair was replicated eight times for a total of 16 plots. We situated this experiment next to one of the pastures used in the RDM experiment. The rainout shelters were constructed with removable, solid, clear polyethylene roofs that fit over a 1.3 × 2.6 m area. After the first germinating rains of the season, we erected the roofs shortly before subsequent rainfall events and removed them afterwards; the roofs were only erect for 10% of the growing season to minimize effects of solar radiation. Shelter run-off was collected and used to irrigate the wet plots.

We maintained rainfall treatments over the course of two growing seasons (October 2012–May 2014). Both years experienced below-average rainfall (510 mm in the 2013 growing season and 398 mm in 2014 compared to average annual rainfall of 730 mm). Due to extreme drought in the 2014 growing season, we irrigated the wet plots using non-chlorinated well water. We monitored the effect on soil moisture using two 15 cm deep time-domain reflectometer (TDR) probes in each plot and 5 cm deep continuous data loggers in half of the plots (EC-5 soil moisture probes; Decagon Devices, Pullman, WA, USA). To confirm that rainfall manipulations generated a dry and wet condition, we used a linear mixed effects model with soil moisture as the response variable, treatment and year as fixed factors, plot nested in block as a random effect using R package NLME (Bates *et al.* 2015) function lme().

Annual rainfall at SFREC ranged between 230 and 1310 mm over the past 50 years (http://sfrec.ucanr.edu/Data/WeatherForage/) and annual rainfall within the East Bay Parks region ranged between 163 and 1041 mm over the last 40 years (http://www.wrcc.dri.edu/). Because we applied rainfall from the dry plots to the wet plots, we estimated that the wet treatments received approximately 1000 mm of rain in 2013 and 800 mm in 2014, reflecting the higher ranges of rainfall at SFREC and East Bay Parks. In addition, the rainfall treatments resulted in significant differences in soil moisture throughout the growing season ($F_{1,108} = 1119$, $P < 0.001$), with on average 28.9 ± 0.48% soil moisture in the wet plots compared to 22.5 ± 1.2% in the dry treatments (Fig. 3).

Within each plot, we measured seed production of *A. barbata*, the most abundant grass, and *E. botrys*, the most abundant forb, within a 0.25 × 0.25 m subplot that was situated to avoid any edge effects. We focused on these two species because they were common in all plots prior to the implementation of the rainfall treatments. Further, they represent a high percentage of the grass and forb cover in the East Bay Parks data set (*Erodium* comprised, on average, 52% of the forb cover and *Avena*, 25% of the exotic annual grass cover). We also expected similar seed production responses to precipitation among the other species within both annual functional groups (Bartolome 1979). While there is likely species-level variation in fecundity patterns, exotic annuals within this system characteristically germinate under a wide range of conditions to maximize their reproduction (Wainwright & Cleland 2013).

Because *Erodium* and *Avena* differ in their phenology, we censused seed production twice: once in late March, when *Erodium* was at peak biomass, and again in late April/early May slightly after *Avena* was at peak. *Erodium* seed pods burst when ripe and contain five fertile filaments. Because *Erodium* seed production was staggered throughout the early spring, we counted the bases of burst seed pods, ripening seed pods and healthy flowers. To assess *Avena* seed production, we counted spikelets that contain two florets that can be identified by papery coverings left behind after seeds drop (Marshall & Jain 1969). Counts were made at the stand level.

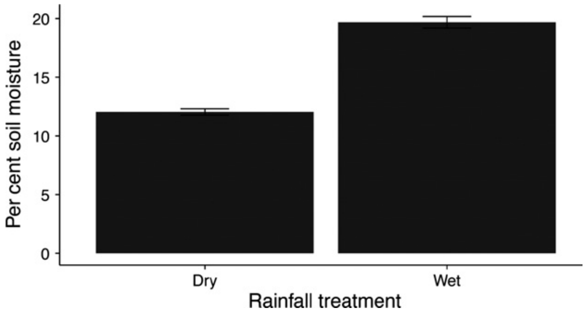

Fig. 3. Rainfall treatment significantly modified soil moisture levels, creating a rainfall effect on species (showing standard error bars).

We analysed seed production using a linear mixed effects model with peak seeds produced as the response variable, species, rainfall treatment and a species × rainfall interaction as explanatory variables and plot nested in block as random effects (function LME in the NLME R package; Bates *et al.* 2015). An interaction effect in which *Avena* seed production was relatively greater in wet plots, whereas *Erodium* seed production was relatively greater in dry plots, would support a seed-rain effect as a potential mechanism of lagged precipitation effects on functional group abundance.

In addition to seed production, we measured peak biomass in each replicate by clipping a 0.25 × 0.25 m subplot in late April/early May, drying the biomass (60 °C for 72 h) and weighing it. To avoid re-harvesting the same area, we sifted the subplot position each year. This allowed us to relate rainfall-driven shifts in biomass with the range in RDM we created in our experiment.

Results

DETECTING A PATTERN OF LAGGED PRECIPITATION EFFECTS

Functional group abundance patterns

Among the three sites, exotic annual grasses ($n = 17$ species) were the dominant functional group, making up 66% of the community across years (CV 0.33). Exotic annual forbs were the subdominant group ($n = 39$ species, 18% of total abundance) with high inter-annual fluctuations (CV 0.801). Combined, exotic annual forbs and grasses comprised 84% of the grassland community, while native species only 16%. Exotic annual forb and grass abundance negatively covaried across years ($Z = -3.34$, $P < 0.001$; d.f. = 7) (Fig. 4).

Functional group responses to precipitation

Both grass and forb abundances were more strongly correlated with previous-year, growing season precipitation than current-year rainfall (Table 1). For example, our annual precipitation model predicted that a one standard deviation (SD) increase in previous-year precipitation would lead to a 30% decrease in forb abundance. In contrast, simulating a one SD increase in current-year precipitation decreased forb abundance by only 4%. Although grasses were less responsive to precipitation overall, a similar difference in current vs. lagged responsiveness occurred. A one SD shift in lagged precipitation predicted a 7% increase in grass abundance, compared to a 1.5% increase with current-year precipitation.

The best-fit seasonal model for grasses and forbs included current and lagged rainfall (Table 1). Grasses responded to current and lagged seasonal precipitation nearly equally, whereas forbs responded more strongly to lagged rainfall

(Table 1). Exotic annual forbs and grasses showed opposite directional responses to seasonal precipitation. Previous dry fall ($T = -3.16$, $P < 0.001$) and spring seasons ($T = -4.77$, $P < 0.001$) were associated with higher forb abundances, while previous wet falls ($T = 2.23$, $P = 0.03$) and springs ($T = 3.13$, $P = 0.002$) were associated with higher grass abundances (Fig. 5). The trend flipped with current-year winter precipitation, resulting in lower grass ($T = -2.55$, $P = 0.01$) and higher forb ($T = 3.30$, $P < 0.001$) abundances (Fig. 5). (See Appendix S2 for figures displaying direct relationships between functional groups and precipitation.)

CHARACTERIZING MECHANISMS OF LAGGED PRECIPITATION EFFECTS IN ANNUAL SYSTEMS

Residual dry matter affects species composition

Species relative cover shifted along the RDM gradient: *Avena* cover declined with lower RDM, while *Erodium* cover increased (RDM × species interaction $F_{5,328} = 2.5$, $P = 0.031$, Fig. 6a). The RDM treatment successfully created a gradient in RDM ($F_{5,39} = 9.47$, $P < 0.001$), with lower RDM levels at the higher mowing/trampling levels (Fig. 6b). RDM also varied among years ($F_{1,95} = 91.02$, $P < 0.001$). The highest average RDM levels in the un-mowed/un-trampled plots occurred in 2010 (517.0 ± 112.6 g m^{-2}), whereas the lowest levels occurred in 2011 (283.4 ± 50.3 g m^{-2}).

Rainfall affects biomass and seed production

Mean biomass in the wet treatment was 480.6 ± 26.4 g m^{-2}, which was similar to the RDM produced in the un-mowed/un-trampled (M1) treatment (Fig. 6b). Mean biomass in the dry treatment was 216.8 ± 19.0 g m^{-2}, corresponding with the RDM levels produced in the moderate mowing/trampling treatments (M3 and M4) (Fig 6b). Given that all the East Bay Parks are grazed with reasonably consistent stocking rates, it

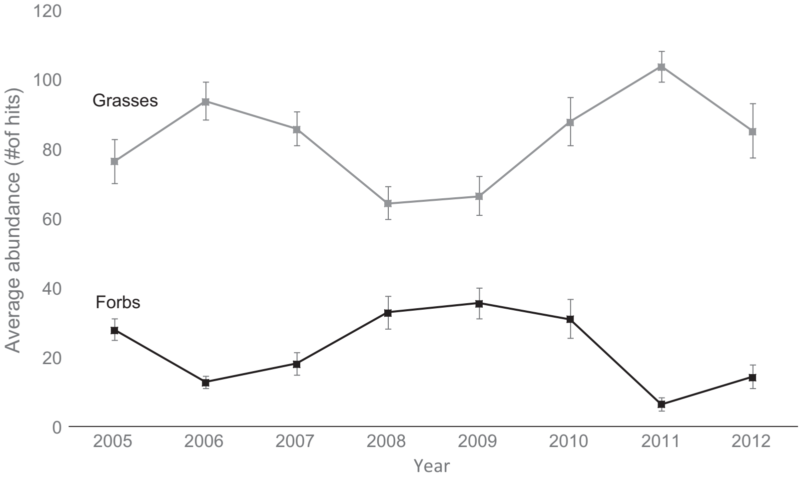

Fig. 4. Average functional group abundance across 8 years (averaged across plots, displaying standard error bars).

Table 1. Generalized linear mixed model (GLMM) regression estimates for exotic annual forb and grass functional groups. Seasonal and annual precipitation models with lowest Akaike information criterion (AIC) values always comprised current and previous-year precipitation. Bolding indicates significant results or most parsimonious model (lowest AIC)

	Exotic annual forbs			Exotic annual grass		
	Current precip.	Lagged precip.	Current and lagged	Current precip.	Lagged precip.	Current and lagged
Seasonal models						
AIC	1132.7	1113.9	**1108.7**	1337.7	1339.8	**1328.6**
Precipitation variables						
Current fall	0.019	–	−0.061	0.017	–	0.046
Current winter	**0.173***	–	**0.224****	**−0.06***	–	**−0.068***
Current spring	**−0.177****	–	−0.081	**0.099****	–	**0.079****
Previous fall	–	**−0.194****	**−0.251****	–	**0.059***	**0.066***
Previous winter	–	0.028	0.072	–	−0.03	−0.039
Previous spring	–	**−0.302****	**−0.275****	–	**0.085****	**0.075****
Annual models						
AIC	1143.7	1122.9	**1122.3**	1353	1346.3	**1345.9**
Precipitation variables						
Annual	0.003	–	0.049	0.024	–	0.016
Previous annual	–	**−0.314****	**−0.32****	–	**0.071****	**0.069****

*$P < 0.05$, **$P < 0.01$.

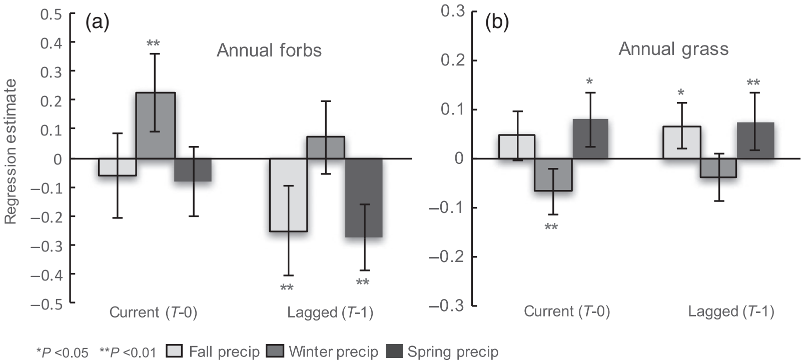

Fig. 5. Regression estimates (with corresponding standard error bars) from models of exotic annual grass and forb abundances. Figure illustrates that lagged seasonal precipitation (T-1) is a strong driver of functional group abundance in annual grasslands.

is likely that the range in RDM associated with rainfall would be similar to our manipulative experiment at SFREC.

Seed composition and production was strongly influenced by precipitation. While total seed production was reduced under dry conditions ($F_{1,52} = 11.5$, $P = 0.0014$), there was a strong differential response by species (species × wet–dry treatment interaction, $F_{1,52} = 4.61$, $P = 0.036$). *Avena* seed production was much lower under dry than wet conditions, whereas *Erodium* seed production did not significantly differ across rainfall treatments (Fig. 7).

Discussion

Understanding precipitation controls on vegetation structure is essential for predicting how climate change will alter communities in the future. Our findings indicated that lagged rainfall effects may help explain a significant proportion of compositional variation in annual plant communities. Although there is a well-documented link between current-year rainfall and annual species composition (e.g. Hobbs & Mooney 1991; Epstein, Burke & Lauenroth 1999; Zavaleta *et al.* 2003), other studies have found that current-year rainfall alone was not a good predictor of composition (Duncan & Woodmansee 1975; Hobbs & Mooney 1995; Dukes & Shaw 2007; Hobbs, Yates & Mooney 2007). By including lagged precipitation in our models, we demonstrated that predictions of abundance improved for annual grasslands. Our experimental work provided support for two pathways creating these lagged effects: rainfall can affect litter production which then modifies recruitment the following growing season, and rainfall can shift seed production, which changes the quantity of germinable seed the next year.

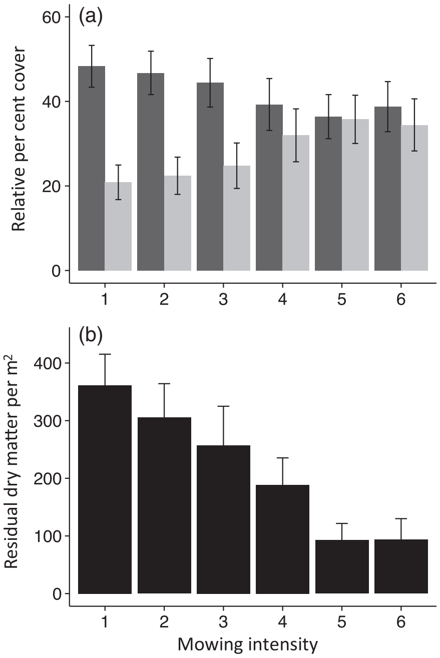

Fig. 6. Residual dry matter (RDM) manipulations shift species composition of forbs and grasses. (a) Mowing/trampling intensity decreased relative per cent cover of grasses and increased forb relative cover. (b) High mowing/trampling intensity reduced RDM. Both graphs show standard error bars.

LAGGED RAINFALL SHIFTS COMMUNITY COMPOSITION

The results from our long-term observational study supported our hypothesis that community composition shifted with lagged precipitation. Both exotic grasses and forbs responded more to total previous-year than total current-year rainfall. Strong lagged effects have also been found in England's perennial-dominated grasslands (Dunnett *et al.* 1998). More common in semi-arid grasslands, however, is an important current-year precipitation effect that is bolstered by including

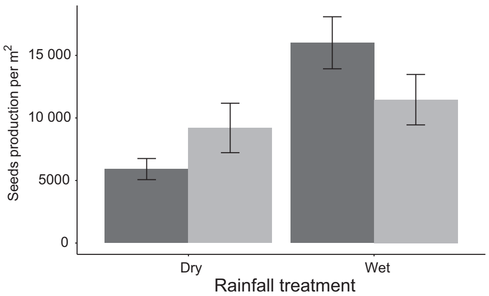

Fig. 7. Seed production of *Avena* and *Erodium* shifted with wet and dry treatments; Rainfall treatments significantly affected *Avena* but not *Erodium* seed production (showing standard error bars).

lagged effects (Oesterheld *et al.* 2001; Wiegand *et al.* 2004). Though the strength of lagged effects in our system is perhaps surprising, the mechanisms discussed below begin to elucidate why lagged precipitation may be critically important for annual grasslands.

Previous-year seasonal rainfall also differentially affected functional group abundance. For example, lagged spring rain and to a lesser degree lagged fall rain were the strongest predictors of forb and grass abundances. These lagged seasonal associations are consistent with results from earlier studies that describe current-year rainfall effects in our system (Murphy 1970; Duncan & Woodmansee 1975; Pitt & Heady 1978). Because both current and lagged precipitation effects were in the same direction, sequential wet or dry conditions may compound to cause stronger, potentially nonlinear changes in community structure (Suttle, Thomsen & Power 2007; Collins *et al.* 2012; Sala *et al.* 2012; Hsu & Adler 2014). It is important to note that although two sequential dry years increased forb abundance in our system, forbs decline after four consecutive dry years (Harrison, Gornish & Copeland 2015). Seasonal rainfall legacies also suggest that biotic carry-over effects are influenced by the timing of rainfall during the previous year, which helps explain why season-specific management can be useful for increasing production and diversity, particularly for exotic species (Stahlheber & D'Antonio 2013).

Overall, lagged rainfall affected forbs more than grasses, indicating that grasses may be less constrained by dry litter and seed production. Thus, directional shifts in rainfall could impact grasses less, which has important implications for management in the face of climate change. Lagged precipitation, however, explained more variation in forb abundance, suggesting that community effects, such as competition with grasses (Seabloom *et al.* 2003) and higher levels of RDM (Suttle, Thomsen & Power 2007), strongly suppress forb growth in wet conditions. Below, we discuss further how precipitation influences biotic legacies that shape annual grasslands.

MECHANISMS OF LAGGED EFFECTS

By isolating the biotic mechanisms creating lagged effects, we can begin to understand how previous-year precipitation differentially impacts species composition in annual grasslands. Vegetative reproduction is commonly cited as an important mechanism for lagged effects in perennial grasslands. Meristem production, including buds, tillers and branches (Dalgleish & Hartnett 2006; Reichmann, Sala & Peters 2012), can create protracted responses to rainfall. Annual plants, however, reproduce primarily through seed and senesce after one growing season, suggesting that the mechanisms of lagged effects for annuals operate through the seed bank and biomass production (Hobbs & Mooney 1995).

By manipulating rainfall, we demonstrated that seed production, particularly for annual exotic grasses such as *Avena,* declined in years with lower rainfall. *Avena* has a transient seed banking strategy (Seabloom *et al.* 2003), and a decline in the number of seeds may limit *Avena* the next year because of the tight connection between seeds produced in 1 year and the amount of germinable seed available the next. Since the majority of *Avena* seeds in the topsoil sprout during the following growing season (Miller & Nalewaja 1990; Russi, Cocks & Roberts 1992), *Avena* has decreased capacity to buffer its abundance than species with more persistent seed banking strategies. Thus, a dry year may reduce *Avena* the following year, while a previous wet year could lead to a corresponding increase.

In contrast, dry conditions did not have a significant impact on the number of *Erodium* seeds, which is consistent with an experimental study in Australia showing that drought stress did not significantly impact *Erodium* fruit production (Cox & Conran 1996). Lower variability in seed production, as well as reduced competition with annual grass seeds, may help explain why a previous dry year increased forb abundance in our long-term study. Persistent seed banking strategies also enable some forbs to capitalize on colonizing windows without relying on the preceding year's seed quantities (Bartolome 1979). Thus, forb seed production and seed banking strategies are consistent with their positive responses to a previous dry year in our long-term study. There may also be additional species-level effects that depend on seed bank longevity and seed production sensitivity to rainfall that our manipulative experiment was unable to capture.

Our RDM experiment provided support for another pathway leading to lagged effects in annual grasslands, where litter from one season influenced recruitment in the following year. In our system, rainfall partially moderates RDM from year to year (Bartolome, Stroud & Heady 1980; Jackson & Bartolome 2007) and these shifts are often associated with different groups of species (Levine, Rees & Bolker 2004; Bartolome *et al.* 2007b; Stahlheber & D'Antonio 2013). The negative lagged precipitation effect on forbs in our long-term study is consistent with our experimental results showing that higher RDM levels suppress forb germination and growth. In contrast, the positive lagged effect on *Avena* highlighted in our long-term study can be linked to higher RDM levels that enhance growth the following year. It is likely that RDM has species-specific effects, and previous research indicates that shifts in RDM may not always positively affect all annual grass species (Amatangelo, Dukes & Field 2008). Additional research teasing apart RDM effects could explain the complexity of lagged effects within functional groups. RDM may also have spatially explicit impacts that are not necessarily related to rainfall. Although biomass production that leads to RDM has long been linked to rainfall patterns (Murphy 1970; Duncan & Woodmansee 1975; Bartolome, Stroud & Heady 1980), other factors such as soil fertility, slope and aspect may be equally if not more important (Bartolome *et al.* 2007b). Thus, across California's environmental gradients, there may be varying impacts of RDM on species composition (Olff & Ritchie 1998; Osem, Perevolotsky & Kigel 2002; Stahlheber & D'Antonio 2013).

CAVEATS AND FUTURE DIRECTIONS

Because our study focused on grasslands with a predominance of exotic annuals, we were unable to describe lagged effects associated with native and perennial species. However, we expect that our results and the mechanisms we identified apply to systems with native annuals. Hobbs & Mooney (1995), for example, found previous-year rainfall linked to a native annual forb, *Lasthenia californica* (L.), in serpentine grasslands. Research on perennial plants also provides insight into the likely mechanisms (e.g. meristem production) (Reichmann, Sala & Peters 2012; Reichmann & Sala 2014) that could be associated with lagged effects on perennials species in our system. In addition, while we expect that litter and seed production are important mechanisms for annual grasslands, studies that assess disturbance regimes (Hobbs & Mooney 1991), herbivory (Peters *et al.* 2006), soil moisture and microbial interactions (Wardle *et al.* 2004) also provide additional evidence for lagged effects on species composition. Our RDM experiment effectively created a dry litter gradient and represents the effects of RDM on species composition (Stein, Harpole & Suding 2016). The design did not include important grazing components such as selective grazing, timing of grazing or faecal deposition. Further experimentation that teases apart these effects would also help describe how grazing could be manipulated to shift species composition the following year. Considering the interactions between precipitation legacies and grazing impacts may also be an interesting extension. For example, how does nutrient deposition and selective grazing shift species composition and do they modify or parallel legacy effects? Finally, air (Pitt & Heady 1978; Chiariello 1989; Zavaleta *et al.* 2003) and soil temperatures (Henry *et al.* 2006) are important controls in our system. Investigating into temperature lags may provide further insight into legacy effects in annual communities.

BROADER IMPLICATIONS

Climate models for semi-arid systems forecast shifts in precipitation regimes, including increased inter- and intra-annual variability and extreme rainfall events (Weltzin *et al.* 2003; Min *et al.* 2011; Durack, Wijffels & Matear 2012). Recent studies indicate that rainfall may increase in our system and extend the growing season (Pan *et al.* 2011; Kendon *et al.* 2014), which could favour annual grasses. There is growing consensus in annual (this study and Hobbs & Mooney 1995), mixed perennial (Sala *et al.* 2012; Sherry *et al.* 2012) and woodland (Weiss *et al.* 2004) systems that including lagged rainfall effects can greatly improve predictions of community responses to shifts in weather patterns. This is particularly true for our annual system, where previous-year total rainfall better predicted annual plant abundance than current-year rainfall. Grass abundance is especially important for rangeland managers, and much effort has been made to develop predictive models (Heady 1956; Bartolome, Stroud & Heady 1980; Bartolome *et al.* 2002). By including lagged precipitation, managers can better predict forage production, regardless of current-year rainfall.

Our results also contribute to an ongoing ecological debate about the relative role of abiotic factors (e.g. precipitation) and biotic factors (e.g. grazing) that influence plant composition (Jackson & Bartolome 2002; Sullivan & Rohde 2002; Vetter 2005). Strong lagged effects in annual systems suggest that grazing and precipitation may affect species composition through shared mechanisms. Specifically, both precipitation and grazing can modify the levels of RDM (Bartolome, Stroud & Heady 1980; Huntsinger, Bartolome & D'Antonio 2007; Jackson & Bartolome 2007), which in turn influences species composition (Hayes & Holl 2003) (though grazing may affect species composition through additional mechanisms, including faecal deposition and selective consumption). Thus, managers may use grazing or mowing to offset the impacts of weather patterns on vegetation. For example, during high rainfall periods grazing may encourage forb cover and greater diversity by reducing grass dominance (Collins *et al.* 1998; Skaer, Graydon & Cushman 2013; Stahlheber & D'Antonio 2013). Alternatively, rangeland managers may be concerned with decreased grass production in dry years (Huntsinger, Bartolome & D'Antonio 2007), which could be mitigated by reducing stocking rates. These recommendations parallel traditional range dogma regarding grazing intensity (Murphy 1970; Duncan & Woodmansee 1975; Bartolome *et al.* 2002) and highlight the importance of flexible grazing practices to maintain grassland plant diversity and production across rainfall conditions (Hayes & Holl 2003; Stahlheber & D'Antonio 2013).

Conclusion

Many studies investigate the high temporal variability of community composition in semi-arid systems, but few have considered how lagged effects contribute to these fluctuations in annual-dominated grasslands. Our results demonstrated that lagged effects were important drivers of species composition and can operate through biotic mechanisms, such as seed and litter production, that are carried over from the previous year. The effect of previous-year precipitation was greater for forbs than grasses, indicating that rainfall-induced biotic effects strongly constrain forb growth and weakly impact grasses. We suggest that understanding the complexity of lagged precipitation effects will be necessary for robust predictions of climate change impacts on annual grasslands and appropriate management responses in the future.

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Conflict of interest

The authors declare they have no conflict of interest.

Data accessibility

East Bay Parks data are available through the Knowledge Network for Biocomplexity (KNB) https://knb.ecoinformatics.org/#view/knb.1183.1 (Dudney *et al.* 2016). Data for the two SFREC studies will be uploaded by September 2017.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Appendix S1. All species present in sampling plots over 8 years.

Appendix S2. Direct relationships of functional groups with precipitation.

Table S1. Correlation coefficients for current and lagged precipitation variables.

Table S2. The coefficient of variation for each functional group across 8 years.