

Consistent ecosystem functional response across precipitation extremes in a sagebrush steppe

Andrew T. Tredennick¹, Andrew R. Kleinhesselink², Bret Taylor³, and Peter B. Adler¹

¹Department of Wildland Resources and the Ecology Center, Utah State University, Logan, Utah 84322

²Department of Ecology and Evolutionary Biology, University of California, Los Angeles, Los Angeles, California 90095

³United States Department of Agriculture, Agriculture Research Station, U.S. Sheep Experiment Station, Dubois, Idaho 83423

Corresponding author:

Andrew T. Tredennick¹

Email address: atredenn@gmail.com

ABSTRACT

Background. Precipitation is predicted to become more variable in the western United States, meaning years of above and below average precipitation will become more common. Periods of extreme precipitation are major drivers of ecosystem functioning in water limited grasslands, but how ecosystems respond to precipitation may change as the duration of above and below average periods increases. Changes in ecosystem functional response could reflect compensatory changes in species composition or species reaching physiological thresholds at extreme precipitation levels.

Methods. We conducted a five year precipitation manipulation experiment in a sagebrush steppe ecosystem in Idaho, US. We used drought and irrigation treatments (approximately 50% decrease/increase) to investigate whether ecosystem functional response remains consistent at extreme precipitation levels. We recorded data on aboveground net primary productivity (ANPP), species abundance, and soil moisture. We fit a generalized linear mixed effects model to determine if the relationship between ANPP and soil moisture differed among treatments. We used nondimensional multivariate scaling to quantify community composition over the five years.

Results. Ecosystem functional response, defined as the relationship between soil moisture and ANPP was similar among drought and control treatments, but the irrigation treatment had a lower slope than the control treatment. However, ANPP response to available soil moisture was weak and uncertain regardless of treatment, with all slopes overlapping zero. There was also no evidence that treatment effects grew over time. Plant community composition was remarkably stable over the course of the experiment and did not differ among treatments.

Discussion. Despite some evidence that ecosystem functional response saturated under extreme wet conditions, the response of ANPP to soil moisture and community compositional changes in this sagebrush steppe system were consistently small. The similarity, or difference, of ecosystem functional response across treatments was not due to compensatory shifts at the plant community level, but instead reflects the weak responses of individual species. Such responses may be due to bet-hedging strategies where species respond weakly to even extreme levels of soil moisture to ensure low variance of long-term success.

1 INTRODUCTION

At a given site, the functional response of aboveground net primary productivity (ANPP) to water availability (e.g., soil moisture) can be characterized by fitting a model to historical observations of ANPP and soil moisture. However, the fitted functional response may provide an incomplete picture because future conditions are likely to be outside the historical range of variability (Smith, 2011). For example,

historical trends may underestimate the potential for the soil moisture-ANPP relationship to saturate if soil moisture is pushed far beyond typical levels. Saturating relationships are actually common (Hsu et al., 2012; Gherardi and Sala, 2015b), perhaps because other resources, like nitrogen, become more limiting in wet years than dry years. Knowing the curvature of the soil moisture-ANPP relationship at extreme precipitation levels is critical for understanding how ecosystems will respond to chronic alterations in water availability.

Another problem with relying on historical ecosystem functional responses is that they are not static. Changes in species identities and abundances can alter an ecosystem's functional response to water availability because different species have different physiological thresholds for producing biomass. Smith et al. (2009) introduced the 'Hierarchical Response Framework' (HRF) for understanding the interplay of community composition and ecosystem functioning in response to resource manipulations over time. In the near term, ecosystem functioning such as ANPP will reflect the physiological responses of individual species to the manipulated resource level. For example, ANPP may decline under simulated drought because the initial community consisted of drought-intolerant species (Hoover et al., 2014). Over longer time spans, ecosystem functioning may recover as new species colonize or initial species reorder in relative abundance. For example, ANPP may initially decline, but eventually rise back to pre-treatment levels once drought-tolerant species become more abundant and compensate for drought-intolerant species (Hoover et al., 2014). It is also possible that ecosystem functioning shifts to a new mean state, reflecting the suite of species in the new community (Knapp et al., 2012).

Manipulating potentially limiting resources, like precipitation, offers a route to understanding how ecosystems will respond to resource levels that fall outside the historical range of variability (Avolio et al., 2015; Gherardi and Sala, 2015a; Knapp et al., 2017). Altering the amount of precipitation over many years should provide insight into the time scales at which water-limited ecosystems respond to chronic resource alteration. Following the HRF, we propose four alternative predictions for the effect of precipitation manipulation on the ecosystem functional response to soil moisture, that is, the soil moisture-ANPP relationship (Fig. 1). The four predictions are based on possible outcomes at the community (e.g., community composition) and ecosystem (e.g., soil moisture-ANPP regression) levels.

First, altered precipitation changes neither ecosystem functional response nor community composition (Fig. 1, top left). In this case, changes in ANPP simply follow the soil moisture-ANPP relationship under ambient conditions. This corresponds to the early phases of the HRF, where ecosystem response is due to the physiological responses of individual species. Second, the ecosystem functional response changes but community composition remains the same (Fig. 1, top right). A saturating soil moisture-ANPP response fits this scenario, where individual species hit physiological thresholds or are limited by some other resource. Third, the ecosystem functional response is consistent but underlying community composition changes (Fig. 1, bottom left). In this case, changes in species' identities or abundances occur in response to altered precipitation levels and species more suited to the new conditions compensate for reduced function of initial species. Fourth, and last, both ecosystem functional response and community composition change (Fig. 1, bottom right). New species, or newly abundant species, with different physiological responses completely reshape the ecosystem functional response.

All four outcomes are possible in any given ecosystem, but the time scales at which the different scenarios play out likely differ (Smith et al., 2009; Wilcox et al., 2016; Knapp et al., 2017). Thus, our task is not to test the validity of the HRF, but rather to amass information on how quickly ecosystem functional responses change in different ecosystems. Likewise, we need to understand whether changes at the ecosystem level are driven by community level changes or individual level responses.

To that end, here we report the results of a five-year precipitation manipulation experiment in a sagebrush steppe grassland. We imposed drought and irrigation treatments (approximately $\pm 50\%$) and measured ecosystem (ANPP) and community (species composition) responses. We focus on how the drought and irrigation treatments affect the relationship between available soil moisture and ANPP, and if community dynamics underlie the ecosystem responses. In particular, we are interested in the consistency of the soil moisture-ANPP relationship among treatments. Is the relationship steeper under the drought treatment, at low soil moisture? Does the relationship saturate under the irrigation treatment, at high soil moisture? To answer these questions we fit a random intercept, random slope model to test whether the regressions differed among treatments. We also analyzed community composition over time, allowing us to place our experimental results within the framework of the HRF and our competing predictions (Fig. 1).

102 2 METHODS

103 2.1 Study Area

104 We conducted our precipitation manipulation experiment in a sagebrush steppe community at the United
105 States Sheep Experimental Station (USSES) near Dubois, Idaho (44.2° N, 112.1° W), 1500 m above
106 sea level. The plant community is dominated by the shrub *Artemisia tripartita* and three perennial
107 bunchgrasses, *Pseudoroegneria spicata*, *Poa secunda*, and *Hesperostipa comata*. During the period of our
108 experiment (2011 – 2015), average mean annual precipitation was 265 mm year⁻¹ and mean monthly
109 temperature ranged from -5.2°C in January to 21.8°C in July. Between 1926 and 1932, range scientists
110 at the USSES established 26 permanent 1 m² quadrats to track vegetation change over time. In 2007,
111 we (well, one of us [P. Adler]) relocated 14 of the original quadrats, six of which were inside a large,
112 permanent livestock enclosure. We use these six plots as control plots that have received no treatment,
113 just ambient precipitation, in the experiment described below.

114 2.2 Precipitation Experiment

115 In spring 2011, we (well, two of us [A. Kleinhesselink and P. Adler]) established 16 new 1 m² plots located
116 in the same enclosure as the six control plots. We avoided areas on steep hill slopes, areas with greater
117 than 20% cover of bare rock, and areas with greater than 10% cover of the shrubs *Purshia tridentata*
118 and/or *Amelanchier utahensis*. We established the new plots in pairs and randomly assigned each plot in a
119 pair to receive a “drought” or “irrigation” treatment.

120 Drought and irrigation treatments were designed to decrease and increase the amount of ambient
121 precipitation by 50%, respectively. To achieve this, we used a system of rain-out shelters and automatic
122 irrigation (Gherardi and Sala, 2013). The rain-out shelters consisted of transparent acrylic shingles 1-1.5
123 m above the ground that covered an area of 2.5 × 2 m. The shingles intercepted approximately 50% of
124 incoming rainfall, which was channeled into 75 liter containers. Captured rainfall was then pumped out
125 of the containers and sprayed on to the adjacent irrigation plot via two suspended sprinklers. Pumping
126 was triggered by float switches once water levels reached about 20 liters. We disconnected the irrigation
127 pumps each fall and reconnected them, often with difficulty, each spring. The rain-out shelters remained
128 in place throughout the year.

129 We monitored soil moisture in four of the drought-irrigation pairs using Decagon Devices (Pullman,
130 Washington) 5TM and EC-5 soil moisture sensors. We installed four sensors around the edges of each plot,
131 two at 5 cm soil depth and two at 25 cm soil depth. We also installed four sensors in areas nearby the four
132 selected plot pairs to measure ambient soil moisture at the same depths. Soil moisture measurements were
133 automatically logged every four hours. We coupled this temporally intensive soil moisture sampling with
134 spatially extensive readings taken at six points within all 16 plots and associated ambient measurement
135 areas. These snapshot data were collected on 06/06/2012, 04/29/2015, 05/07/2015, 06/09/2015, and
136 05/10/2016 using a handheld EC-5 sensor.

137 Analyzing the response to experimental treatments was complicated by the fact that we did not directly
138 monitor soil moisture in each plot on each day of the experiment. Only a subset of plots were equipped
139 with soil moisture sensors, and within those plots, one or more of the sensors frequently failed to collect
140 data. To remedy these problems, and to produce average daily soil moisture values for the ambient,
141 drought, and irrigation conditions, we used a statistical model to predict the average treatment effects on
142 soil moisture during the course of the experiment.

143 We first averaged the observed soil moisture for each day and within each plot. Then we standardized
144 the averages within each plot group by subtracting the average ambient soil moisture in that plot group
145 and dividing by the standard deviation of the ambient soil moisture in that plot group. We then found the
146 difference between the standardized ambient soil moisture and the standardized drought and irrigation
147 soil moisture within each plot group. These transformations ensured that the treatment effects in each plot
148 were appropriately scaled by the local ambient conditions within each plot group.

149 We then modeled the daily deviation from ambient conditions of the drought and irrigation treatments
150 using a linear mixed effects model with independent variables for treatment, season (winter, spring,
151 summer, fall), rainfall, and all two-way interactions. Rainy days were defined as any day in which
152 precipitation was recorded and average temperature was above 3°C. The day immediately following
153 rainfall was also classified as rainy. We fit the model using the ‘lme4::lmer()’ function (Bates et al., 2015)

in R (R Core Team, 2016), with random effects for plot group and date. We weighted observations by the number of unique sensors or spot measurements that were taken in each plot on that day. We then used the model to predict the average daily soil moisture in the treated plots based on the average daily ambient soil moisture. We could only predict soil moisture in the treated plots on days for which we took at least one ambient soil moisture measurement.

2.3 Data Collection

We estimated aboveground net primary productivity (ANPP) using a radiometer to relate ground reflectance to plant biomass (see Byrne et al., 2011, for a review). We recorded ground reflectance at four wavelengths, two associated with red reflectance (626 nm and 652 nm) and two associated with near-infrared reflectance (875 nm and 859 nm). At each plot in each year, we took four readings of ground reflectances at the above wavelengths. We also took readings in 12 (2015), 15 (2012, 2013, 2014), or 16 (2016) calibration plots adjacent to the experimental site, in which we harvested all aboveground biomass, dried it to a constant weight at 60°C, and weighed it to estimate ANPP.

For each plot and year, we averaged the four readings for each wavelength and then calculated a greenness index based on the same bands used to calculate NDVI using the MODIS and AVHRR bands for NDVI. To convert the greenness index to ANPP we regressed the greenness index against the dry biomass weight from the ten calibration plots. We fit regressions to MODIS-based index and AVHRR-based index for each year and retained the regression with the better fit. Using the best regression equation for each year, we predicted ANPP (Appendix 1).

Species composition data came from two sources: yearly census maps for each plot made using a pantograph (Hill, 1920) and yearly counts of annual species in each plot. From those maps, we have data on the density of all annuals and perennials forbs, basal cover of perennial grasses, and canopy cover of shrubs. We made a large plot-treatment-year by species matrix, where columns were filled with either basal cover or density, depending on the measurement made for the particular species. So we could analyze the different types of data together, we standardized the values in each column. This puts all abundance values on the same scale, meaning that common and rare species are weighted equally. Nonetheless, if we assume that rare species will respond more than common ones, then this approach is anti-conservative for detecting community change. This means that our approach is biased toward detecting compositional changes.

2.4 Data Analysis

Our main goal was to test whether the relationship between ANPP and soil moisture differed among the drought, control, and irrigation treatments. Based on our own observations and previous work at our study site (Blaisdell, 1958; Dalglish et al., 2011; Adler et al., 2012), we chose to use cumulative volumetric water content from March through June as our metric of soil moisture (hereafter referred to as ‘VWC’). To achieve this goal, we fit a generalized linear mixed effects regression model with $\log(\text{ANPP})$ as the response variable and VWC and treatment as fixed effects. Plot and year of treatment were included as random effects to account for non-independence of observations, as described below. We log-transformed ANPP to account for heteroscedasticity. Both $\log(\text{ANPP})$ and VWC were standardized to have mean 0 and unit variance before fitting the model [i.e., $(x_i - \bar{x})/\sigma_x$].

Our model is defined as follows:

$$\mu_i = \beta \mathbf{x}_i + \gamma_{j(i)} \mathbf{z}_i + \eta_t, \quad (1)$$

$$\mathbf{y} \sim \text{Normal}(\boldsymbol{\mu}, \sigma^2), \quad (2)$$

where μ_i is the deterministic prediction from the regression model for observation i , which is associated with plot j and treatment year t . β is the vector of coefficients for the fixed effects in the design matrix \mathbf{X} . Each row of the design matrix represents a single observation (\mathbf{x}_i) and is a vector with the following elements: 1 for the intercept, a binary 0 or 1 if the treatment is “drought”, a binary 0 or 1 if the treatment is “irrigation”, the scaled value of VWC, binary “drought” value times VWC, and binary “irrigation” value times VWC. Thus, our model treats “control” observations as the main treatment and then estimates intercept and slope offsets for the “drought” and “irrigation” treatments. In reference to our model, the hypotheses we wish to test are:

202 **H1** The coefficient for drought \times VWC is positive and different from zero.

203 **H2** The coefficient for irrigation \times VWC is negative and different from zero.

204 To account for the fact that observations within plots and years are not independent, we include two
205 random effects. Specifically, we include plot-specific offsets ($\boldsymbol{\gamma}$) for the intercept and slope terms and
206 year-specific intercept offsets (η_t). The covariate vector \mathbf{z}_i for each observation i has two elements: a 1
207 for the intercept and the scaled value of VWC for that plot and year. The plot-specific coefficients are
208 modeled hierarchically, where plot level coefficients are drawn from a multivariate normal distribution
209 with mean 0 and a variance-covariance structure that allows the intercept and slope terms to be correlated:

$$\boldsymbol{\gamma}_{j(i)} \sim \text{MVN}(0, \Sigma), \quad (3)$$

210 where Σ is the variance-covariance matrix and $j(i)$ reads as “plot j associated with observation i ”. The
211 random year effects ($\boldsymbol{\eta}$) are drawn from a normal prior with mean 0 and standard deviation σ_{year} , which
212 was drawn from a half-cauchy distribution. A full description of our model is in Appendix 2.

213 We fit the model using a Bayesian approach, obtaining posterior estimates of all unknowns via the
214 No-U-Turn Hamiltonian Monte Carlo sampler in Stan (Stan Development Team, 2016b). We used the R
215 package ‘rstan’ (Stan Development Team, 2016a) to link R (R Core Team, 2016) to Stan. We obtained
216 samples from the posterior distribution for all model parameters from four parallel MCMC chains run
217 for 10,000 iterations, saving every 10th sample. Trace plots of all parameters were visually inspected to
218 ensure well-mixed chains and convergence. We also made sure all scale reduction factors (\hat{R}) were less
219 than 1.1.

220 To see if community composition differed among treatments through time, we used non-dimensional
221 multivariate scaling (NMDS) based on Bray-Curtis distances. For each year of the experiment, we first
222 calculated Bray-Curtis distances among all plots, and then extracted those distances for use in the NMDS.
223 Because we standardized species’ abundances, some values were negative, which is not allowed for
224 calculating Bray-Curtis distances. We simply added ‘2’ to each abundance value to ensure all values
225 were greater than zero. We plotted the first two axes of NMDS scores to see if community composition
226 overlapped, or not, among treatments in each year. We used the ‘metaMDS()’ function in the R package
227 ‘vegan’ (Oksanen, 2016) to calculate Bray-Curtis distances and then to run the NMDS analysis. We used
228 the ‘vegan::adonis()’ function (Oksanen, 2016) to perform permutational multivariate analysis of variance
229 to test whether treatment plots formed distinct groupings. To test whether treatment plots were equally
230 dispersed, or not, we used the ‘vegan::betadisper’ function (Oksanen, 2016).

231 All R code and data necessary to reproduce our analysis has been archived on Figshare (*link here after*
232 *acceptance*) and released on GitHub ([https://github.com/atredennick/usses_water/](https://github.com/atredennick/usses_water/releases/v0.1)
233 [releases/v0.1](https://github.com/atredennick/usses_water/releases/v0.1)). We also include annotated Stan code in our model description in Appendix 2.

234 3 RESULTS

235 Three of our five treatment years fell in years of below average rainfall (Fig. 2A). Thus, those three years
236 represent a lower magnitude of absolute change in precipitation experienced by the treatments. Averaged
237 across treatments, ANPP varied from a minimum of 74.5 g m⁻² in 2014 to a maximum of 237.1 g m⁻² in
238 2016 (Fig. 2C). ANPP was slightly higher in irrigation plots and slightly lower in drought plots (Fig. 2C),
239 corresponding to estimated soil volumetric water content (VWC) differences among treatments (Fig. 2B).
240 Such differences in soil VWC indicate our treatment infrastructure was successful.

241 Cumulative March-June soil moisture had a weak positive effect on ANPP (Table 1; Fig. 3), but the
242 effect is associated with high uncertainty, with credible intervals that overlap zero, regardless of treatment
243 (Table 1). Ecosystem functional response was similar among treatments (Table 1; Fig. 3B), but there is
244 evidence that the slope for the irrigation treatment is less than the slope for the control treatment. This
245 evidence comes from interpreting the posterior distribution of the slope offset for the irrigation treatment,
246 from which we calculate a 98% probability that the estimate is less than zero (Fig. 3A, right panel).
247 There was no evidence that the treatment effects became more important over time because there was no
248 directional trend in the random year effects (Fig. A2-2).

249 Community composition was similar among treatments. In no year did community composition among
250 treatments not overlap, and they were equally dispersed in all years (Table 2; Fig. 5). Likewise, community

composition was remarkably stable over time, with no evidence of divergence among treatments (Table 2; Fig. 5).

4 DISCUSSION

Ecosystem response to precipitation extremes depends on the physiological responses of constituent species and the rate at which community composition shifts to favor species better able to take advantage of, or cope with, new resource levels (Smith et al., 2009). Previous work has shown that community compositional shifts can be both rapid, on the order of years (Hoover et al., 2014), and slow, on order of decades (Knapp et al., 2012; Wilcox et al., 2016). Thus, a lingering question is how the time scales of ecosystem response and community change differ among ecosystems, which can be answered by manipulating precipitation to reach extreme levels.

The results of our five year experiment in a sagebrush steppe conform to two of our four predictions, depending on treatment. Under chronic drought, neither ecosystem functional response nor community composition changed (Fig. 1, top left). But under irrigation, ecosystem functional response was different from the control treatment while community composition remained unchanged (Fig. 1, top right). Thus, we found some evidence for a saturating response at high water availability (Fig. 3), but the response of ANPP to soil moisture was weak overall, regardless of treatment (Table 1).

The similarity of ecosystem functional response (Fig. 3) and community composition (Fig. 5) between drought and control treatments is surprising because grasslands generally, and sagebrush steppe specifically, are considered water-limited systems. Indeed, we expected ecosystem functional response, community composition, or both to change under the drought treatment, landing us in any box of Fig. 1 *except* the top left. So, why did our drought treatment fail to induce ecosystem or community responses? We can think of three reasons; two are limitations of our study, and one is the life history traits of the species in our focal communities. We first discuss the potential limitations of our study, and then discuss the biological explanation.

First, it could be that our manipulations were not large enough to induce a response. That is, maybe a 50% decrease/increase in any given year is not abnormal given our site's historical range of variability (Knapp et al., 2017). We cannot definitively rule out this possibility, but we have reason to believe our manipulations *should* have been large enough. Using the methods described by Lemoine et al. (2016), we calculated the percent reduction and increase of mean growing season precipitation necessary to reach the 1% and 99% extremes of the historical precipitation regime at our site. The 1% quantile of precipitation at our site is 110 mm, a 47% reduction from the mean, and the 99% quantile is 414 mm, a 77% increase from mean growing season precipitation (Appendix 3). Thus, our drought treatment represented extreme precipitation amounts, especially in years where ambient precipitation was below average (Fig. 2A). The irrigation treatment may have been too small, yet that is the treatment where we observed an effect (Fig. 3).

Second, ANPP at our site may be influenced by factors beyond the window of soil moisture we included in our statistical model. For example, temperature can impact ANPP directly (Epstein et al., 1997) and by exacerbating the effects of soil moisture (De Boeck et al., 2011). Measurements of soil moisture likely contain a signal of temperature, through its impact on evaporation and infiltration, but the measurements will not capture the direct effect of temperature on metabolic and physiological processes. Likewise, we did not redistribute snow across our treatments in the winter, and snow melt may spur early spring growth. These statistical issues of missing potentially important covariates could explain the weak and uncertain relationship we observed between soil moisture and ANPP.

Third, the life history traits of the dominant species in our study ecosystem may explain the consistent but weak and uncertain effect of soil moisture on ANPP (Fig. 3). Species that live in variable environments, such as cold deserts, must have strategies to ensure long-term success as conditions vary. One strategy is bet hedging, where species forego short-term gains to reduce the variance of long-term success (Seger, 1987). In other words, species do the same thing every year, with only minimal response to environmental conditions. The dry and variable environment of the sagebrush steppe has likely selected for bet hedging species that can maintain function at low water availability and have weak responses to high water availability. In so doing, the dominant species in our ecosystem avoid “boom and bust” cycles, which corresponds to the weak effect of soil moisture on ANPP (i.e., the credible intervals for β_1 overlapping zero), even at precipitation extremes.

304 Another strategy to deal with variable environmental conditions is avoidance, which would result
305 in a consistent ecosystem functional response at low soil moisture. The perennial plants in this cold
306 desert ecosystem are tolerant to drought conditions (Bazzaz, 1979; Franks, 2011, A.R. Kleinhesselink,
307 unpublished data). For example, many of the perennial grasses in our focal ecosystem avoid drought stress
308 by growing early in the growing season (Blaisdell, 1958, A.R. Kleinhesselink, personal observation).
309 Likewise, the dominant shrub in our focal ecosystem, *Artemisia tripartita*, has access to water deep in the
310 soil profile thanks to a deep root system (Kulmatiski et al., 2017).

311 In conclusion, our results suggest that five years of $\pm 50\%$ ambient precipitation is not enough
312 to induce a shift in ecosystem functional response in a sagebrush steppe. This is likely because the
313 species in our focal plant community are tolerant of drought conditions and bet hedgers in wet conditions,
314 maintaining relatively consistent responses to interannual variation in precipitation to avoid booms and
315 busts. Longer time series of chronic precipitation alteration may reveal plant community shifts that we did
316 not observe (e.g., Wilcox et al., 2016), in which case species that do not bet hedge may gain prominence
317 and dominate the ecosystem functional response. Our results suggest compositional shifts would have the
318 largest impact at high rainfall because the current community maintained consistent ecosystem functional
319 response at very low water availability.

320 **5 ACKNOWLEDGEMENTS**

321 We thank the many summer research technicians who collected the data reported in this paper and the
322 US Experimental Sheep Station for facilitating work on their property. We also thank Susan Durham for
323 clarifying our thinking on the statistical analyses and Kevin Wilcox for helpful discussions on analyzing
324 community composition data.

325 **6 FUNDING**

326 This research was supported by the Utah Agricultural Experiment Station, Utah State University, and
327 approved as journal paper number XXXX. The research was also supported by the National Science
328 Foundation, through a Postdoctoral Research Fellowship in Biology and Mathematics to ATT (DBI-
329 1400370), a Graduate Research Fellowship to ARK, and grants DEB-1353078 and DEB-1054040 to
330 PBA.

331 **7 AUTHOR CONTRIBUTIONS**

- 332 • Andrew T. Tredennick collected data, analyzed the data, wrote the paper, prepared figures and/or
333 tables, reviewed drafts of the paper.
- 334 • Andrew R. Kleinhesselink conceived and designed the experiments, performed the experiments,
335 collected data, analyzed the data, reviewed drafts of the paper.
- 336 • Bret Taylor contributed reagents/materials/analysis tools, reviewed drafts of the paper.
- 337 • Peter B. Adler conceived and designed the experiments, performed the experiments, collected data,
338 analyzed the data, reviewed drafts of the paper.

339 **8 SUPPLEMENTAL INFORMATION**

340 **Appendix 1.** Additional methods and information on estimating aboveground net primary productivity.

341 **Appendix 2.** Details of the hierarchical Bayesian model, Fig. A2-1, and Fig. A2-2.

342 **Appendix 3.** Details on analysis of precipitation historical range of variability and Fig. A3-1.

9 TABLES

Table 1. Summary statistics from the posterior distributions of coefficients for each treatment.

Coefficient	Treatment	Posterior Mean	Posterior Median	Lower 95% BCI	Upper 95% BCI
Intercept	Control	0.02	0.03	-1.06	1.01
Intercept	Drought	-0.04	-0.04	-1.39	1.21
Intercept	Irrigation	-0.13	-0.11	-1.35	1.09
Slope	Control	0.63	0.64	-0.33	1.61
Slope	Drought	0.46	0.47	-0.59	1.52
Slope	Irrigation	0.26	0.26	-0.60	1.12

Table 2. Results from statistical tests for clustering and dispersion of community composition among precipitation treatments. ‘adonis’ tests whether treatments form unique clusters in multidimensional space; ‘betadisper’ tests whether treatments have similar dispersion. For both tests, P values greater than 0.05 indicate there is no support that the treatments differ.

Year	Test	n	d.f.	F	P
2011	adonis	21	2	1.02	0.42
2011	betadisper	21	2	2.23	0.14
2012	adonis	22	2	1.10	0.34
2012	betadisper	22	2	0.21	0.81
2013	adonis	22	2	1.23	0.14
2013	betadisper	22	2	0.28	0.76
2014	adonis	22	2	0.95	0.54
2014	betadisper	22	2	0.35	0.71
2015	adonis	21	2	1.05	0.40
2015	betadisper	21	2	3.01	0.07
2016	adonis	21	2	1.07	0.33
2016	betadisper	21	2	0.50	0.62

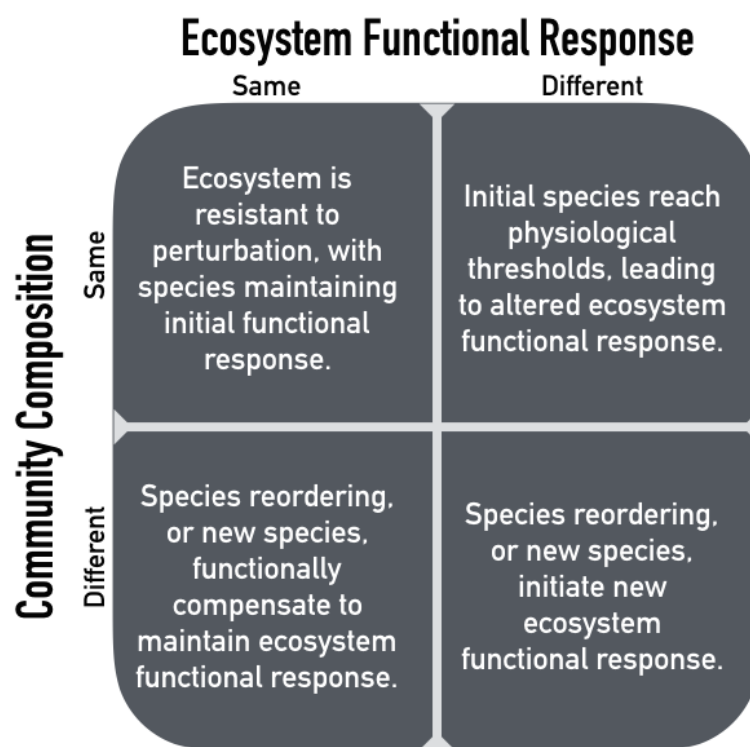


Figure 1. Possible outcomes of chronic resource alteration.

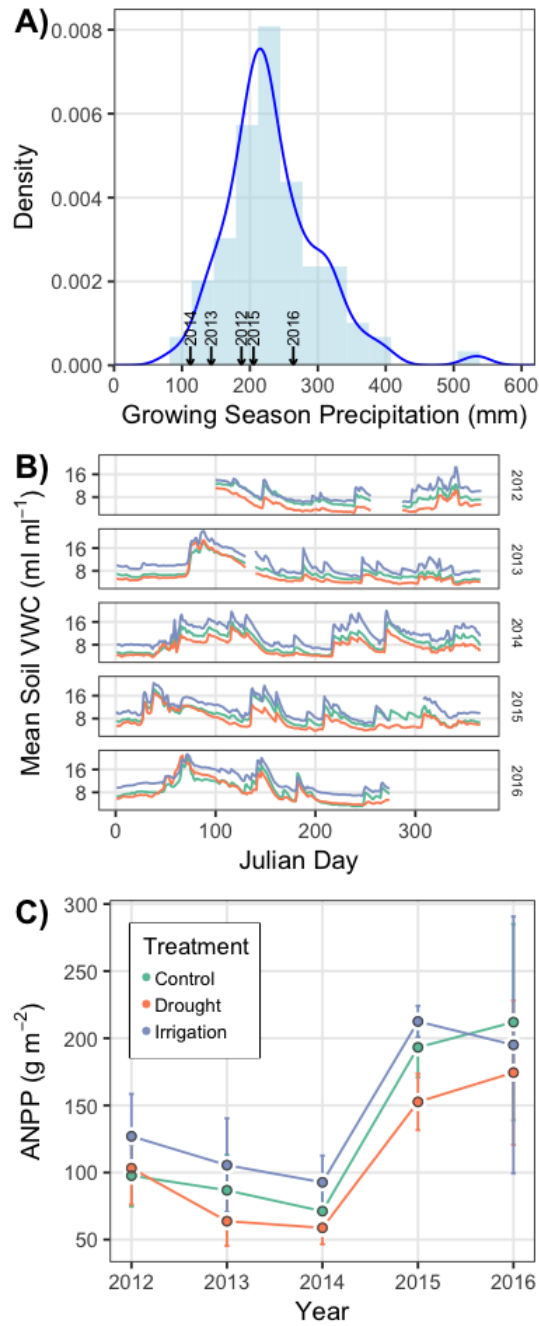


Figure 2. (A) Probability density of historical precipitation from 1926-2016, with the years of the experiment shown with arrows on the x -axis. (B) Observed soil volumetric water content (VWC) over the course of the experiment. (C) Mean (points) ANPP and its standard deviation (error bars) for each year of the experiment.

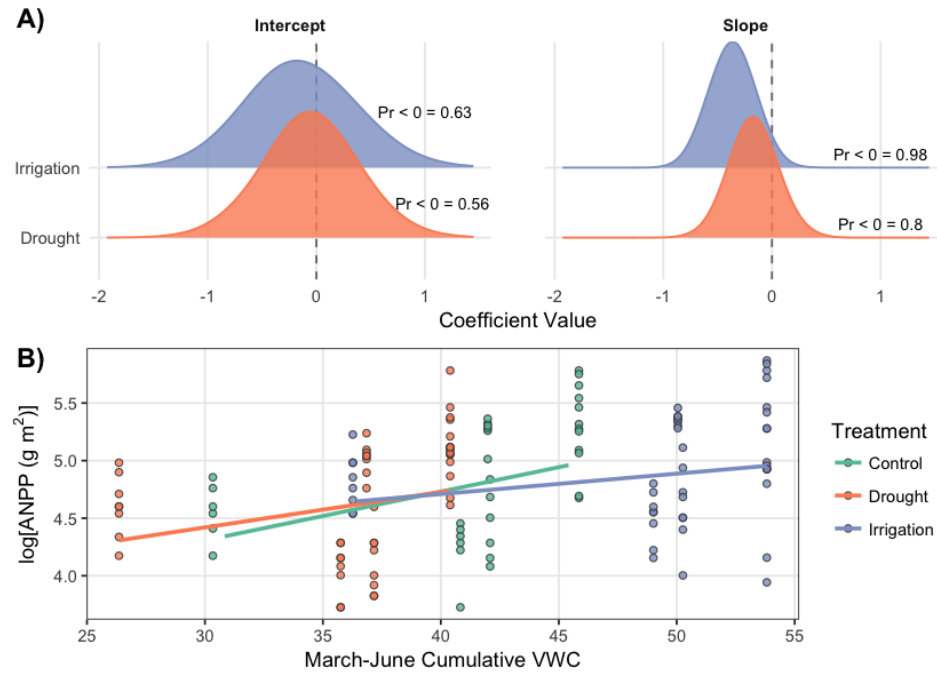


Figure 3. Results from the generalized linear mixed effects model. (A) Posterior distributions of the intercept and slope offsets for the drought and irrigation treatments. Offsets indicate the amount to which the coefficients for drought or irrigation treatments differ from the control treatment estimates. Probabilities (“ $Pr < 0 =$ ”) for each distribution indicate the probability that coefficient is less than zero. Probabilities greater than 0.95 indicate strong support for the coefficient being less than zero. We only show the one-tailed probability for the value being less than zero because the median of each distribution is less than zero. Kernel bandwidths of posterior densities were adjusted by a factor of 5 for visual clarity. (B) Scatterplot of the data and model estimates shown as solid lines. Model estimates come from treatment level coefficients (colored lines). Note that we show $\log[ANPP]$ on the y-axis of panel B; this same plot can be seen on the arithmetic scale in supporting material Fig. A2-1.

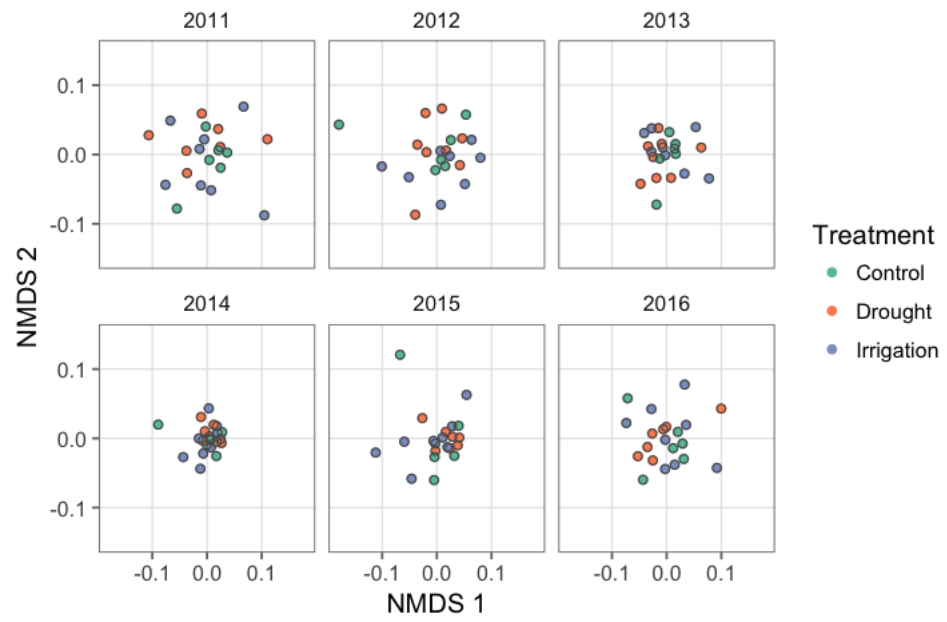


Figure 4. Nonmetric multidimensional scaling scores representing plant communities in each plot, colored by treatment.

345 References

- 346 Adler, P. B., Dalgleish, H. J., and Ellner, S. P. (2012). Forecasting plant community impacts of climate
347 variability and change: when do competitive interactions matter? *Journal of Ecology*, 100:478–487.
- 348 Avolio, M. L., Pierre, K. J. L., Houseman, G. R., Koerner, S. E., Grman, E., Isbell, F., Johnson, D. S.,
349 and Wilcox, K. R. (2015). A framework for quantifying the magnitude and variability of community
350 responses to global change drivers. *Ecosphere*, 6(12):1–14.
- 351 Bates, D., Maechler, M., Bolker, B., and Walker, S. (2015). Fitting linear mixed-effects models using
352 lme4.
- 353 Bazzaz, F. (1979). The Physiological Ecology of Plant Succession. *Annual Review of Ecology and*
354 *Systematics*, 10:351–371.
- 355 Blaisdell, J. P. (1958). Seasonal development and yield of native plants on the upper snake river plains
356 and their relation to certain climate factors. *United States Department of Agriculture Technical Bulletin*
357 *No. 1190*.
- 358 Byrne, K. M., Lauenroth, W. K., Adler, P. B., and Byrne, C. M. (2011). Estimating Aboveground Net
359 Primary Production in Grasslands: A Comparison of Nondestructive Methods. *Rangeland Ecology and*
360 *Management*, 64(5):498–505.
- 361 Dalgleish, H. J., Koons, D. N., Hooten, M. B., Moffet, C. A., and Adler, P. B. (2011). Climate influences
362 the demography of three dominant sagebrush steppe plants. *Ecology*, 92(1):75–85.
- 363 De Boeck, H. J., Dreesen, F. E., Janssens, I. A., and Nijs, I. (2011). Whole-system responses of
364 experimental plant communities to climate extremes imposed in different seasons. *New Phytologist*,
365 189(3):806–817.
- 366 Epstein, H. E., Lauenroth, W. K., and Burke, I. C. (1997). Effects of temperature and soil texture on
367 ANPP in the U.S. Great plains. *Ecology*, 78(8):2628–2631.
- 368 Franks, S. J. (2011). Plasticity and evolution in drought avoidance and escape in the annual plant *Brassica*
369 *rapa*. *New Phytologist*, 190(1):249–257.
- 370 Gherardi, L. A. and Sala, O. E. (2013). Automated rainfall manipulation system: a reliable and inexpensive
371 tool for ecologists. *Ecosphere*, 4(2):1–10.
- 372 Gherardi, L. A. and Sala, O. E. (2015a). Enhanced interannual precipitation variability increases
373 plant functional diversity that in turn ameliorates negative impact on productivity. *Ecology Letters*,
374 18(12):1293–1300.
- 375 Gherardi, L. A. and Sala, O. E. (2015b). Enhanced precipitation variability decreases grass- and increases
376 shrub-productivity. *Proceedings of the National Academy of Sciences*, 112(41):12735–12740.
- 377 Hill, R. R. (1920). Charting Quadrats with a Pantograph. *Ecology*, 1(4):270–273.
- 378 Hoover, D. L., Knapp, A. K., and Smith, M. D. (2014). Resistance and resilience of a grassland ecosystem
379 to climate extremes. *Ecology*, 95(9):2646–2656.
- 380 Hsu, J. S., Powell, J., and Adler, P. B. (2012). Sensitivity of mean annual primary production to
381 precipitation. *Global Change Biology*, 18(7):2246–2255.
- 382 Knapp, A. K., Avolio, M. L., Beier, C., Carroll, C. J. W., Collins, S. L., Dukes, J. S., Fraser, L. H., Griffin-
383 Nolan, R. J., Hoover, D. L., Jentsch, A., Loik, M. E., Phillips, R. P., Post, A. K., Sala, O. E., Slette, I. J.,
384 Yahdjian, L., and Smith, M. D. (2017). Pushing precipitation to the extremes in distributed experiments:
385 recommendations for simulating wet and dry years. *Global Change Biology*, 23(5):1774–1782.
- 386 Knapp, A. K., Briggs, J. M., and Smith, M. D. (2012). Community stability does not preclude ecosystem
387 sensitivity to chronic resource alteration. *Functional Ecology*, 26(6):1231–1233.
- 388 Kulmatiski, A., Adler, P. B., Stark, J. M., and Tredennick, A. T. (2017). Water and nitrogen uptake are
389 better associated with resource availability than root biomass. *Ecosphere*, 8(3).
- 390 Lemoine, N. P., Sheffield, J., Dukes, J. S., Knapp, A. K., and Smith, M. D. (2016). Terrestrial Precipitation
391 Analysis (TPA): A resource for characterizing long-term precipitation regimes and extremes. *Methods*
392 *in Ecology and Evolution*, 7(11):1396–1401.
- 393 Oksanen, J. (2016). *Vegan: ecological diversity*.
- 394 R Core Team (2016). *R: A Language and Environment for Statistical Computing*. Vienna, Austria.
- 395 Seger, J. (1987). What is bet-hedging? In Harvey, P. and Partridge, L., editors, *Oxford surveys in*
396 *evolutionary biology*, pages 182–211. Oxford University Press, Oxford.
- 397 Smith, M. (2011). An ecological perspective on extreme climatic events: A synthetic definition and
398 framework to guide future research. *Journal of Ecology*, 99(3):656–663.

- 399 Smith, M. D., Knapp, A. K., and Collins, S. L. (2009). A framework for assessing ecosystem dynamics in
400 response to chronic resource alterations induced by global change. *Ecology*, 90(12):3279–3289.
- 401 Stan Development Team (2016a). Rstan: the R interface to Stan, Version 2.14.1.
- 402 Stan Development Team (2016b). Stan: A C++ Library for Probability and Sampling, Version 2.14.1.
- 403 Wilcox, K. R., Blair, J. M., Smith, M. D., and Knapp, A. K. (2016). Does ecosystem sensitivity to
404 precipitation at the site-level conform to regional-scale predictions? *Ecology*, 97(3):561–568.