

# Ecosystem and community resistance to five years of drought and deluge in a sagebrush steppe

Andrew T. Tredennick<sup>1,\*</sup>, Andrew R. Kleinheesselink<sup>2</sup>, and Peter B. Adler<sup>1</sup>

<sup>1</sup>*Department of Wildland Resources and the Ecology Center, Utah State University, Logan, Utah*

<sup>2</sup>*Department of Ecology and Evolutionary Biology, University of California, Los Angeles, Los Angeles, California*

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## Abstract

Precipitation is predicted to become more variable in the western U.S., meaning years of above and below average precipitation will become more common. Such periods of drought and deluge could become major drivers of plant community dynamics and ecosystem functioning. Here we report the results of a five-year experiment where we used drought and irrigation treatments (50% decrease/increase) to see how a sagebrush steppe plant community in Idaho will respond to future climate changes. The ecosystem was surprisingly resistant to both drought and irrigation. Aboveground net primary productivity (ANPP) responded positively to ambient growing season precipitation, but the response did not vary across treatments. There was also no evidence that treatment effects grew over time. The similarity of ecosystem functioning was not due to compensatory shifts at the plant community level, where species composition among treatments was similar and remarkably stable over the five years. At least in the short-term, ecosystem functioning and community composition in this sagebrush steppe system is resistant to increases and decreases in growing season precipitation.

*Key words: drought, aboveground net primary productivity, ecosystem resistance, climate change, species composition, sagebrush steppe*

## 1 Introduction

2 As the rate of climate change accelerates, ecologists are being pressed to forecast its impacts  
3 on ecosystem functions and services. Making such forecasts faces two challenges. First, future  
4 conditions are likely to be outside the historical range of variability (???), meaning we cannot  
5 simply look to the past to predict the future. Second, ecosystems will likely exhibit unique  
6 responses to climate change induced resource alterations (e.g., ???), meaning we cannot simply look  
7 across space to predict the future. These two challenges motivate the use of *in situ* experimental  
8 manipulations of resource availability (Avolio et al. 2015).

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\*Corresponding author; e-mail: atredenn@gmail.com

9 Manipulating potentially limiting resources offers a route to understanding how ecosystems  
10 will respond to resource levels that fall outside the historical range of variability (???). Chronic  
11 alterations to resource availability should cause community composition to shift over time, the  
12 focal ecosystem is sensitive to the manipulated resource. Species' relative abundances are expected  
13 to re-order and, eventually, some species will be lost from the local community and new species  
14 will be gained (Smith et al. 2009, Avolio et al. 2015). On the heels of changes in community  
15 composition, subsequent changes in the level of ecosystem functioning may occur.

16 Smith et al. (2009) introduced the 'Hierarchical Response Framework' for understanding the  
17 interplay of community composition and ecosystem functioning in response to resource manipula-  
18 tions over time. In the near term, ecosystem functioning such as annual net primary productivity  
19 (ANPP) will reflect the physiological responses of individual species to the manipulated resource  
20 level. For example, ANPP may decline under simulated drought because the initial community  
21 consisted of drought-intolerant species. Over longer time spans, ecosystem functioning may  
22 recover as new species, better suited to take advantage of the new resource regime, colonize local  
23 communities. For example, ANPP may initially decline, but eventually rise back to pre-treatment  
24 levels once drought-tolerant species colonize. It is also possible that ecosystem functioning shifts  
25 to a new mean state, reflective of the suite of species in the new community.

26 Much of the research on ecosystem and community responses to global climate change  
27 has focused on grassland systems, where water is typically a limiting resource. The sensitivity  
28 of ANPP to water availability in grasslands has been characterized spatially (across sites) and  
29 temporally (within sites). Spatially, there is a strong positive relationship between the amount of  
30 precipitation at a given site and mean ANPP (Knapp citation). Temporally, however, the response  
31 of ANPP to interannual precipitation variability is much weaker (Hsu and Adler).

32 In many areas of the western United States, precipitation is likely to become more variable.  
33 This will result in swings back-and-forth between multiyear periods of above and above average  
34 precipitation. An obvious question is, how will semiarid ecosystems respond to periods of drought  
35 and deluge? A naive expectation is that alterations in precipitation, and subsequently available  
36 soil moisture, should cause changes in plant community composition and increase or decrease  
37 ANPP depending on the direction of precipitation change. But our emerging qualitative  
38 understanding suggests an alternative expectation: altering soil moisture may have little to no  
39 effect on plant community composition and ecosystem functioning. This expectation stems from  
40 the fact that precipitation is already a variable resource in semiarid systems, meaning the plant  
41 community is not sensitive to realistic increases/decreases in precipitation.

42 Here we test our qualitative understanding of how altering precipitation will impact a  
43 sagebrush steppe ecosystem by imposing drought and irrigation for five years. In particular, we  
44 test the following competing predictions:

**P1.** Altering precipitation will favor certain species over others, resulting in a shift in the plant community composition. ANPP will increase (irrigation) or decrease (drought), and the treatment effects will get stronger over time (a treatment×year interaction).

**P2.** Altering precipitation will not favor certain species and plant community composition will not change. ANPP will increase (irrigation) or decrease (drought), and the treatment effects will get stronger over time.

Note that both predictions assume ANPP will respond to precipitation alteration. Under **P1**, ANPP response stems directly from plant community shifts to species able to take advantage of the new precipitation regime. Under **P2**, ANPP response stems from all species responding similarly to changes in precipitation.

## Materials and Methods

### Study Area

We conducted our precipitation manipulation experiment at the United States Sheep Experimental Station (USSES) near Dubois, Idaho (44.2° N, 112.1° W), 1500 m above sea level. The vegetation is typical of high elevation sagebrush steppe. The plant community is dominated by the shrub *Artemesia tripartita* and three perennial bunchgrasses, *Pseudoroegneria spicata*, *Poa secunda*, and *Hesperostipa comata*. During the period of our experiment (2011 – 2015), average mean annual precipitation was 265 mm year<sup>-1</sup> and mean monthly temperature ranged from -5.2°C in January to 21.8°C in July.

### Precipitation Experiment

Between 1926 and 1932, range scientists at the USSES established 26 permanent 1 m<sup>2</sup> quadrats to track vegetation change over time. In 2007, we (well, one of us [P. Adler]) relocated 14 of the original quadrats, six of which were inside a large, permanent livestock enclosure. We use these six plots as control plots that have received no treatment, just ambient precipitation. In spring 2011, we (well, two of us [A. Kleinhesselink and P. Adler]) established 16 new 1 m<sup>2</sup> plots. We avoided areas on steep hill slopes, areas with greater than 20% cover of bare rock, and areas with greater than 10% cover of the shrubs *Purshia tridentata* and/or *Amelanchier utahensis*. We established the new plots in pairs and randomly assigned each plot in a pair to receive a “drought” or “irrigation” treatment.

Drought and irrigation treatments were designed to decrease and increase the amount of ambient precipitation by 50%, respectively. To achieve this, we used a system of rain-out shelters and automatic irrigation (Gherardi and Sala 2013). The rain-out shelters consisted of

transparent acrylic shingles 1-1.5 m above the ground that covered an area of  $2.5 \times 2$  m. The shingles intercepted approximately 50% of incoming rainfall, which was channeled into 75 liter containers. Captured rainfall was then pumped out of the containers and sprayed on to the adjacent irrigation plot via two suspended sprinklers. Pumping was triggered by float switches once water levels reached about 20 liters. We disconnected the irrigation pumps each fall and reconnected them, often with difficulty, each spring. The rain-out shelters remained in place throughout the year.

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

[ANDY: paragraph here on SOILWAT. Is this the right thing to show/do? See Fig. 1C.]

## 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 (xxx and xxx) and two associated with near-infrared reflectance (xxx and xxx). At each plot in each year, we took four readings of ground reflectances at the above wavelengths. We also took readings in ten 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 NDVI using the MODIS and AVHRR algorithms. To convert NDVI to ANPP we regressed NDVI against the dry biomass weight from the ten calibration plots. We fit regressions to MODIS-based NDVI and AVHRR-based NDVI 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 annual census maps for each plot made using a pantograph (Hill 1920). The maps record the spatial location and size of each individual plant. Using those annual maps, we aggregated over individuals to calculate total basal cover for each species in each plot.

## 111 Data Analysis

112 Our goal was to test whether the relationship between ANPP and growing season precipitation  
 113 (hereafter, precipitation) differed among the drought, control, and irrigation treatments. To achieve  
 114 this goal, we fit a multi-level random intercept and random slope regression with log(ANPP) as  
 115 the response variable and precipitation as the sole predictor. We fit the model under a Bayesian  
 116 framework, allowing us to test for treatment differences by comparing the posterior distributions  
 117 of the treatment-level coefficients (e.g., Tredennick et al. 2013). Both log(ANPP) and precipitation  
 118 were standardized to have mean 0 and unit variance before fitting the model [i.e.,  $(x_i - \bar{x})/\sigma_x$ ].

119 Our multi-level model has three grouping levels for coefficients, representing the nested  
 120 structure of the data: (i) overall coefficients, (ii) treatment coefficients, and (iii) plot coefficients.  
 121 Each subsequent level is drawn from the distribution of coefficients at the previous level. Formally,  
 122 our model is defined as follows:

$$\mu_{i(j(k))} = \beta_{0,j(k)} + \beta_{1,j(k)}x_i, \quad (1)$$

$$y_{i(j(k))} \sim \text{Normal}(\mu_{i(j(k))}, \sigma_k^2), \quad (2)$$

123 where  $\mu_{i(j(k))}$  is the deterministic prediction from the regression model for observation  $i$  for plot  $j$   
 124 associated with treatment  $k$ ,  $\beta_{0,j(k)}$  is the intercept for plot  $j$  associated with treatment  $k$ ,  $\beta_{1,j(k)}$  is  
 125 the slope term for the effect of precipitation for plot  $j$  associated with treatment  $k$ , and  $\sigma_k^2$  is the  
 126 process variance for treatment  $k$ . Data include the standardized log(ANPP) observations ( $y_{i(j(k))}$ )  
 127 and precipitation ( $x_i$ ). Although we include observation subscript  $i$  on the  $x$ s, observations within  
 128 a year all share the same precipitation values.

129 The intercept and slope terms are modeled hierarchically to account for the non-  
 130 independence of observations across years within plots and to allow us to test the hypothesis that  
 131 our treatments alter the ANPP-precipitation relationship. As noted above, plot-level coefficients  
 132 are drawn from treatment-level coefficients, which are drawn from overall coefficients. We  
 133 also include a covariance structure among the intercept and slope at each level. Formally, our  
 134 hierarchical structure is as follows, where we drop the intercept (0) and slope (1) subscripts and  
 135 instead refer to a vector of coefficients,  $\beta$ :

$$\beta_{j(k)} \sim \text{MVN}(\beta_k, \Sigma(k)), \quad (3)$$

$$\beta_k \sim \text{MVN}(\beta, \Sigma), \quad (4)$$

$$\beta \sim \text{Normal}(0, 1), \quad (5)$$

136 where  $\beta_{j(k)}$  is the vector of regression coefficients (intercept and slope) for plot  $j$  associated with  
 137 treatment  $k$ ,  $\beta_k$  is the vector of coefficients for each treatment, and  $\beta$  is the vector of overall

coefficients. The plot- and treatment-level coefficients are drawn from multivariate normal distributions with covariance matrix  $\Sigma$ . For the plot-level coefficients, each treatment has its own variance-covariance matrix (i.e.,  $\Sigma(k)$ ). The overall coefficients are drawn from a normal prior with mean 0 and standard deviation 1. A full description of model is in Appendix 2.

We fit the above model for the drought and irrigation treatments independently because we are only interested in comparing each treatment to the control, not to each other. We fit the model using a Bayesian approach, obtaining posterior estimates of all unknowns via the No-U-Turn Hamiltonian Monte Carlo sampler in Stan (Stan Development Team 2016a). We used the R package ‘rstan’ (Stan Development Team 2016b) to link R (R Core Team 2016) to Stan. We obtained samples from the posterior distribution for all model parameters from four parallel MCMC chains run for 10,000 iterations, saving every 10<sup>th</sup> sample. Traceplots of all parameters were visually inspected to ensure well-mixed chains and convergence. We also made sure all scale reduction factors ( $\hat{R}$ ) were less than 1.1.

To see if community composition differed among treatments through time, we used non-dimensional multivariate scaling (NMDS) based on Bray-Curtis distances. For each year of the experiment, we first calculated Bray-Curtis distances among all plots, and then extracted those distances for use in the NMDS. We plotted the first two axes of NMDS scores to see if community composition overlapped, or not, among treatments in each year. We used functions in the R package ‘vegan’ (Oksanen 2016) to calculate Bray-Curtis distances and then to run the NMDS analysis. Lastly, we examined rank clocks of species’ abundances through time to assess the stability of community composition over the course of the experiment (Collins et al. 2008). Rank clocks were made using ‘ggplot2’ (Wickham 2009) and R code from Hallett et al. (2016).

All R code and data necessary to reproduce our analysis has been archived on Figshare (*link here after acceptance*) and released on GitHub ([https://github.com/atredennick/usses\\_water/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.

## Results

Three of our five treatment years fell in years of below average rainfall (Fig. 1A). Thus, those three years represent a lower magnitude of absolute change in precipitation experienced by the treatments. Averaged across treatments, ANPP varied from a minimum of 74.5 g m<sup>-2</sup> in 2014 to a maximum of 237.1 g m<sup>-2</sup> in 2016 (Fig. 1C). ANPP was slightly higher in irrigation plots and slightly lower in drought plots (Fig. 1C), corresponding to estimated soil volumetric water content (VWC) differences among treatments (Fig. 1B). Such differences in soil VWC indicate our treatment infrastructure was successful.

Growing season precipitation had a positive effect on ANPP (mean of  $\beta_1 = 0.67$ ; 80% BCI =

0.24, 1.10; 95% BCI = -0.11, 1.34) (Fig. 1D). Average ANPP was similar among treatments (similar intercepts, Fig. 2A), as was the effect of precipitation (similar slopes, Fig. 2B). In an average precipitation year (i.e.,  $x = 0$  in Eq. 1), the probability that ANPP in a drought plot is less than ANPP in a control plot was 0.58, and the probability that ANPP in an irrigation plot is higher than in a control plot was 0.57. In other words, the posterior distributions of  $\beta_0(\text{control}) - \beta_0(\text{drought})$  and  $\beta_0(\text{control}) - \beta_0(\text{drought})$  broadly overlapped zero. There was also no evidence that the treatment effects became more important over time because differences between average treatment and control plots were centered on zero regardless of year of the experiment (Fig. 3).

Community composition was similar among treatments, whether looking at basal cover or density (Fig. 4). Likewise, community composition was remarkably stable over time, with no evidence of divergence among treatments (Fig. 4). Species' abundances and ranks showed little deviation over the five-year experiment, regardless of treatment (Fig. 5).

## Discussion

We manipulated growing season precipitation for five years in a sagebrush steppe to reach the extremes of the historical distribution of precipitation (Fig. 1A). In so doing, we aimed to understand how this ecosystem might respond to periods of relatively novel precipitation regimes. Our results suggest that ecosystem functioning, as measured by annual net primary productivity, and community composition are not sensitive to the precipitation manipulations we imposed.

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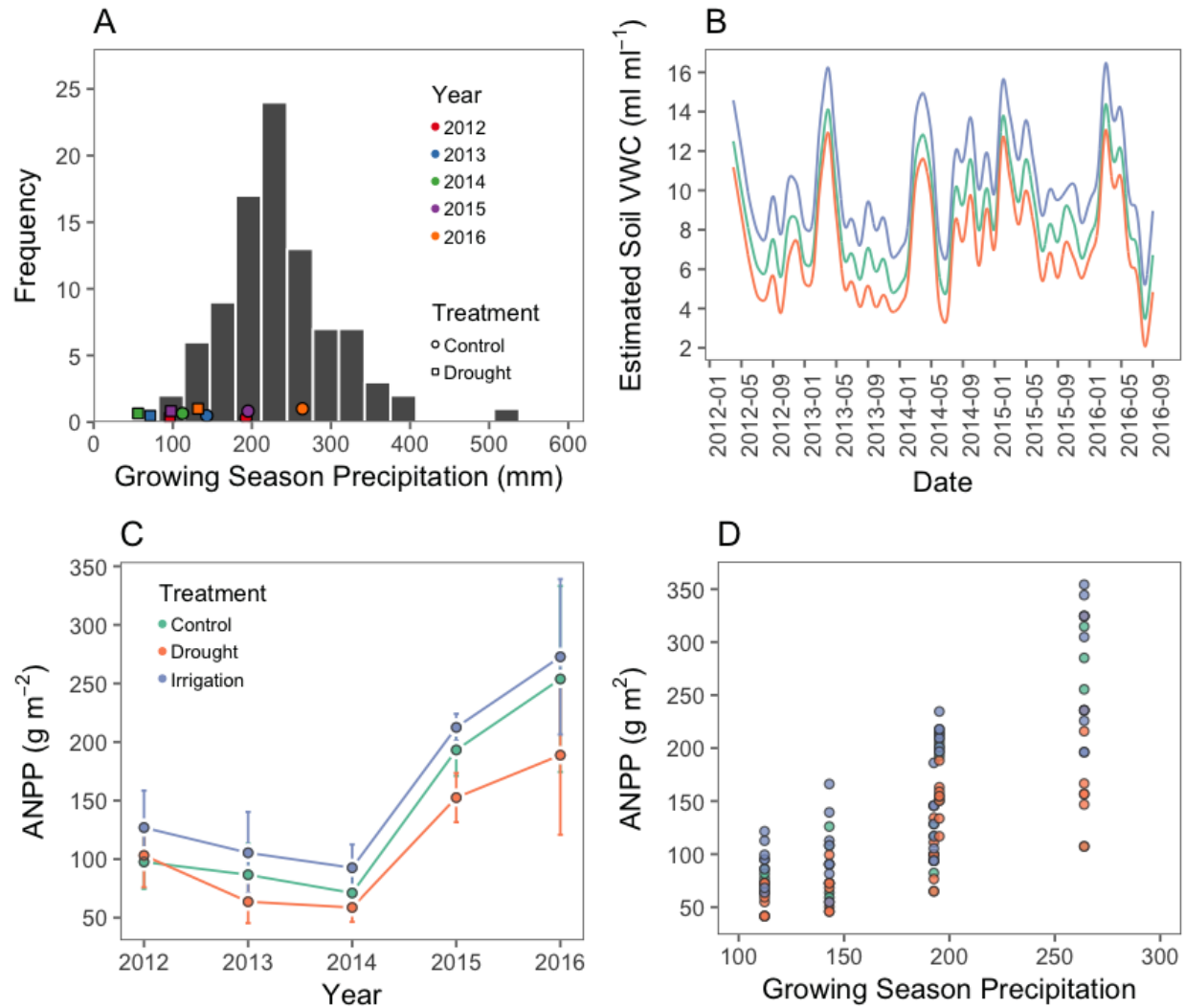


Figure 1: (A) Histogram of historical precipitation from 1926-2016, with the years of the experiment overlaid as colored points. "Drought" treatments (squares) are shown as a 50% reduction from the observed precipitation. "Irrigation" treatment precipitation levels are not shown. (B) Monthly average estimated soil volumetric water content (VWC) from SOILWAT model fit using soil moisture data from experimental plots. (C) Mean (points) ANPP and its standard deviation (error bars) for each year of the experiment. (D) Scatterplot of ANPP versus growing season precipitation.



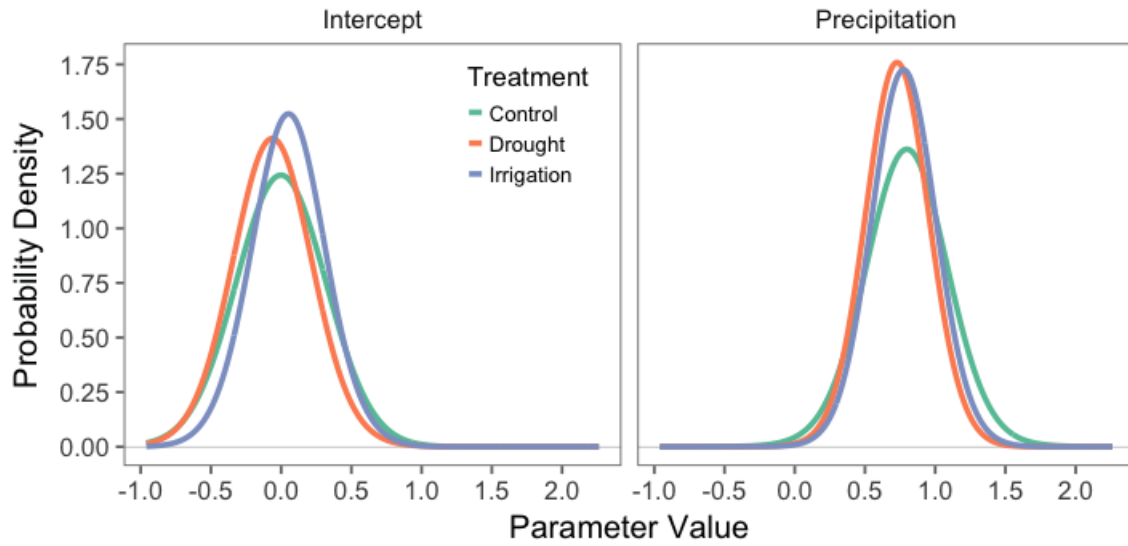


Figure 2: (A) Relationship between ANPP and growing season precipitation over the course of the experiment. Regression lines are independent linear fits for each treatment for visual clarity of the mean trends. (B) Posterior medians (points), 80% BCIs (heavy lines), and 95% BCIs (light lines) of effects from the fitted repeated measures generalized linear mixed-effects model for each treatment-control comparison. BCI refers to 'Bayesian Credible Interval', which is the upper and lower quantiles of the posterior distribution at the specified level.

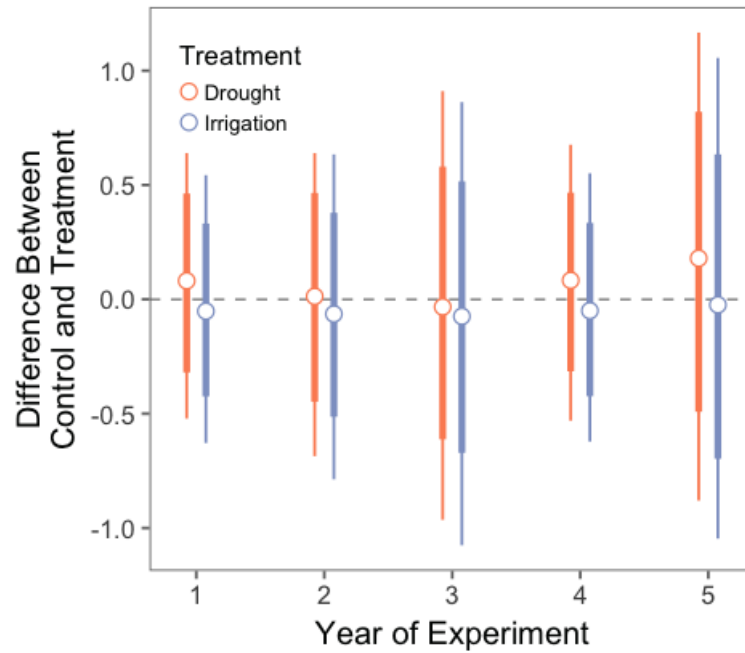


Figure 3: Posterior medians (points), 80% BCIs (heavy lines), and 95% BCIs (light lines) of the difference between  $\log(\text{ANPP})$  in control and treatment plots over time. BCI refers to 'Bayesian Credible Interval', which are the upper and lower quantiles of the posterior distribution at the specified level.

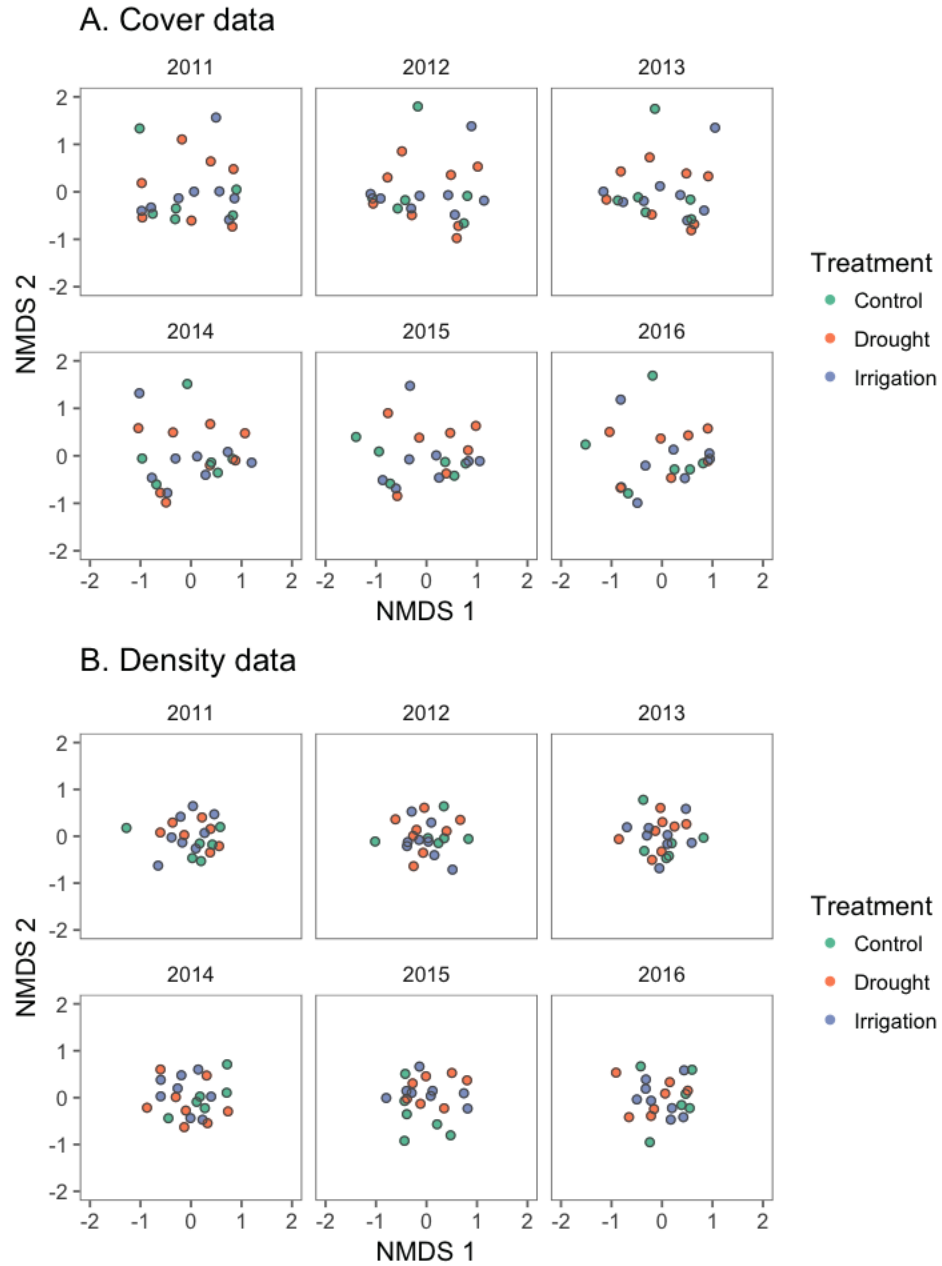
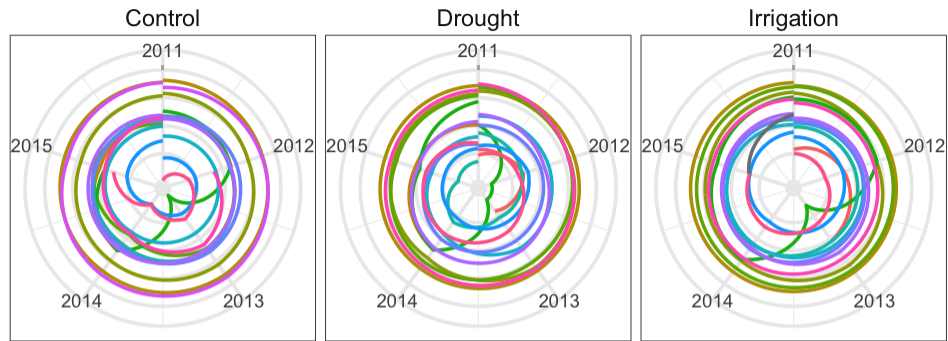


Figure 4: Nonmetric multidimensional scaling scores representing plant communities in each plot, colored by treatment. (A) NMDS results using basal cover data; (B) NMDS results using individual density data. 2011 is a pre-treatment year.

### A. All species



### B. Dominant species

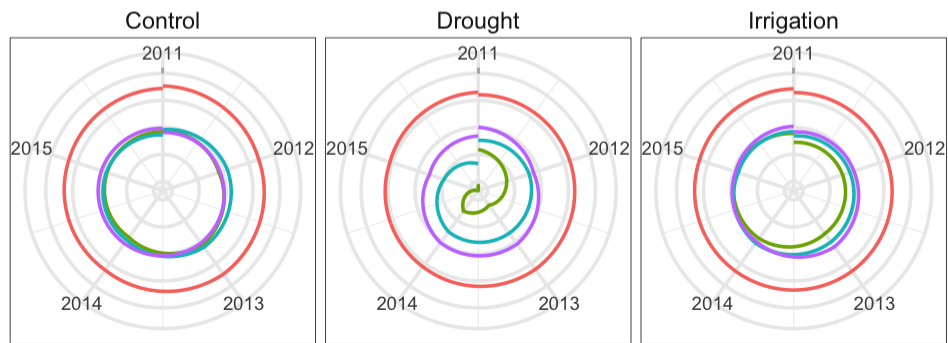


Figure 5: Rank clocks of average species' basal cover by treatment. (A) All species. (B) Dominant species. Cover is log-transformed to improve visualization of species with low cover.

## References

- Avolio, M. L., K. J. L. Pierre, G. R. Houseman, S. E. Koerner, E. Grman, F. Isbell, D. S. Johnson, and K. R. Wilcox. 2015. A framework for quantifying the magnitude and variability of community responses to global change drivers. *Ecosphere* 6:1–14.
- Byrne, K. M., W. K. Lauenroth, P. B. Adler, and C. M. Byrne. 2011. Estimating Aboveground Net Primary Production in Grasslands: A Comparison of Nondestructive Methods. *Rangeland Ecology & Management* 64:498–505.
- Collins, S. L., K. N. Suding, E. E. Cleland, M. Batty, S. C. Pennings, K. L. Gross, J. B. Grace, L. Gough, J. E. Fargione, and C. M. Clark. 2008. Rank clocks and plant community dynamics. *Ecology* 89:3534–3541.
- Gherardi, L. A., and O. E. Sala. 2013. Automated rainfall manipulation system: a reliable and inexpensive tool for ecologists. *Ecosphere* 4:1–10.
- Hallett, L. M., S. K. Jones, A. A. M. MacDonald, M. B. Jones, D. F. B. Flynn, J. Ripplinger, P. Slaughter, C. Gries, and S. L. Collins. 2016. codyn: An r package of community dynamics metrics. *Methods in Ecology and Evolution* 7:1146–1151.
- Hill, R. R. 1920. Charting Quadrats with a Pantograph. *Ecology* 1:270–273.
- Oksanen, J. 2016. *Vegan: ecological diversity*.
- R Core Team. 2016. *R: A Language and Environment for Statistical Computing*. Vienna, Austria.
- Smith, M. D., A. K. Knapp, and S. L. Collins. 2009. A framework for assessing ecosystem dynamics in response to chronic resource alterations induced by global change. *Ecology* 90:3279–3289.
- Stan Development Team. 2016a. *Stan: A C++ Library for Probability and Sampling, Version 2.14.1*.
- Stan Development Team. 2016b. *Rstan: the R interface to Stan, Version 2.14.1*.
- Tredennick, A. T., L. P. Bentley, and N. P. Hanan. 2013. Allometric convergence in savanna trees and implications for the use of plant scaling models in variable ecosystems. *PLoS One* 8:e58241.
- Wickham, H. 2009. *ggplot2: Elegant Graphics for Data Analysis*. Springer-Verlag, New York, NY.