

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

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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 (Smith 2011), meaning we
5 cannot 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., Byrne et al. 2017), meaning we
7 cannot simply look across space to predict the future. These two challenges motivate the use of *in*
8 *situ* experimental manipulations of resource availability (Avolio et al. 2015).

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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 (Knapp et
11 al. 2017). Chronic alterations to resource availability should cause community composition to
12 shift over time, the focal ecosystem is sensitive to the manipulated resource. Species' relative
13 abundances are expected to re-order and, eventually, some species will be lost from the local
14 community and new species will be gained (Smith et al. 2009, Avolio et al. 2015). On the heels of
15 changes in community composition, subsequent changes in the level of ecosystem functioning
16 may occur.

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

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

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

43 Here we test our qualitative understanding of how altering precipitation will impact a
44 sagebrush steppe ecosystem by imposing drought and irrigation for five years. In particular, we
45 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, average mean annual precipitation was xxx mm and mean monthly temperature ranged from -x°C in January to x°C in July.

Precipitation Experiment

Between 1926 and 1932, range scientists at the USSES established 26 permanent 1 m² 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 recieved no treatment, just ambient precipitation. In spring 2011, we (well, two of us [A. Kleinhesselink and P. Adler]) established 16 new 1 m² 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 × 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 $\log(\text{ANPP})$ 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 $\log(\text{ANPP})$ 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:

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

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

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 σ_k^2 is the
 126 process variance for treatment k . Data include the standardized $\log(\text{ANPP})$ 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. Note that we drop the intercept (0) and slope (1) subscripts and
 135 instead refer to a vector of coefficients, β .

$$\beta_{j(k)} \sim \mathcal{N}(\beta_k, \Sigma(k)), \quad (3)$$

$$\beta_k \sim \mathcal{N}(\beta, \Sigma), \quad (4)$$

$$\beta \sim \mathcal{N}(0, 1). \quad (5)$$

136 We fit the above model for the drought and irrigation treatments independently because
 137 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.

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). We also include annotated Stan code in our model description in Appendix 1.

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 xxx g m⁻² in 2014 to a maximum of xxx g m⁻² in 2016 (Fig. 1B). ANPP was slightly higher in irrigation plots and slightly lower in drought plots (Fig. 1B), corresponding to estimated soil volumetric water content (VWC) differences among treatments (Fig. 1C). Such differences in soil VWC indicate our treatment infrastructure was successful.

Growing season precipitation had a positive effect on ANPP (Fig. 2 and Table 1), but ANPP over the entirety of the experiment was not different from control plots for either drought ($\text{Pr}(\text{Drought} < \text{Control}) \leq 0.95$) or irrigation ($\text{Pr}(\text{Irrigation} > \text{Control}) \leq 0.95$) treatments (Fig. 2 and Table 1). There was also no evidence that the treatment effects became more important over time ($\text{Pr}(\text{Treatment} \times \text{Year}) \leq 0.95$; Fig. 2B and Table 1).

Community composition was similar among treatments, whether looking at basal cover or density (Fig. 3). Likewise, community composition was remarkably stable over time, with no evidence of divergence among treatments (Fig. 3). Species’ abundances and ranks showed no deviation over the five-year experiment, regardless of treatment (Fig. 4).

Discussion

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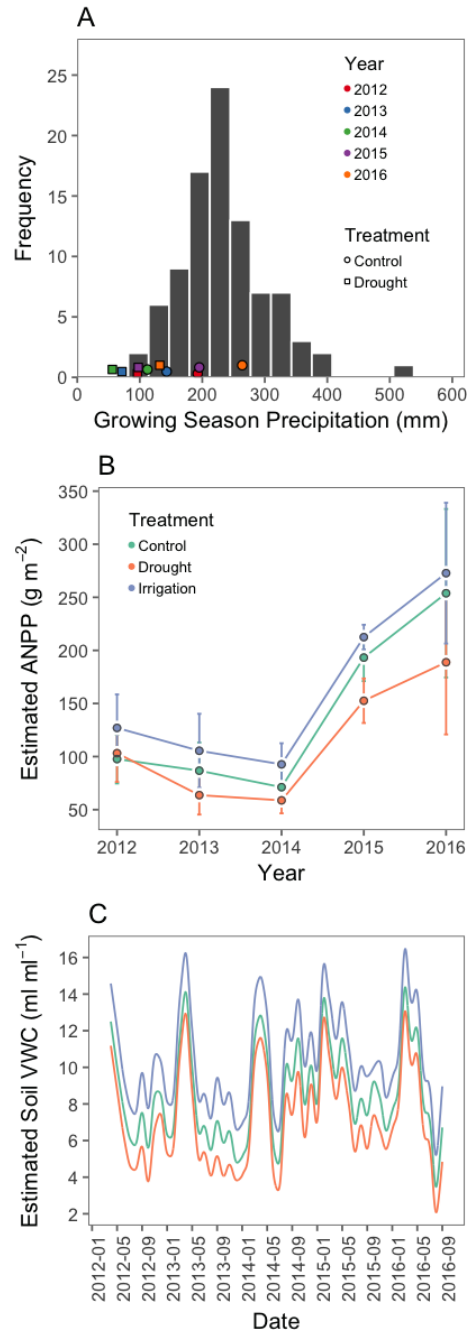


Figure 1: (A) Histogram of historical precipitation from 1926-2016, with the years of the experiment overlaid as colored points. “Drought” treatments (squares) are shown as a 50% reduction from the observed precipitation. “Irrigation” treatment precipitation levels are not shown. (B) Mean (points) ANPP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

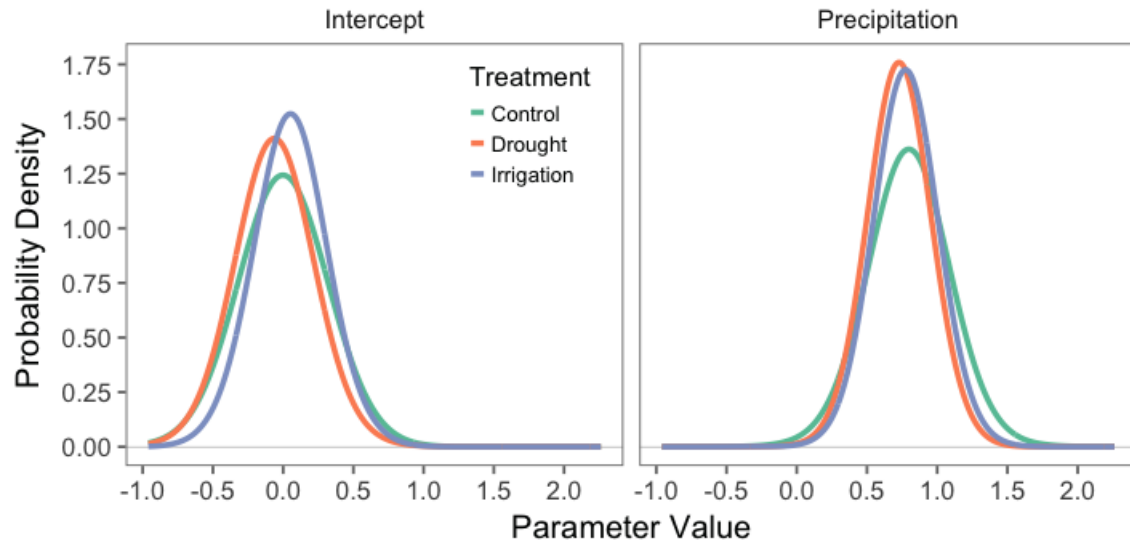


Figure 2: (A) Relationship between ANPP and growing season precipitation over the course of the experiment. Regression lines are independent linear fits for each treatment for visual clarity of the mean trends. (B) Posterior medians (points), 80% BCIs (heavy lines), and 95% BCIs (light lines) of effects 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.

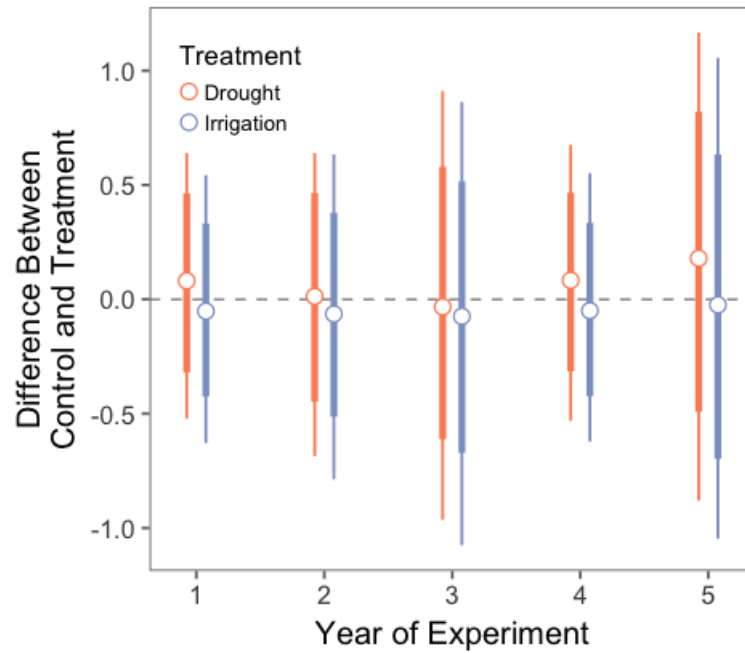


Figure 3: Posterior medians (points), 80% BCIs (heavy lines), and 95% BCIs (light lines) of the difference between log(ANPP) in control and treatment plots over time. BCI refers to 'Bayesian Credible Interval', which is the upper and lower quantiles of the posterior distribution at the specified level.

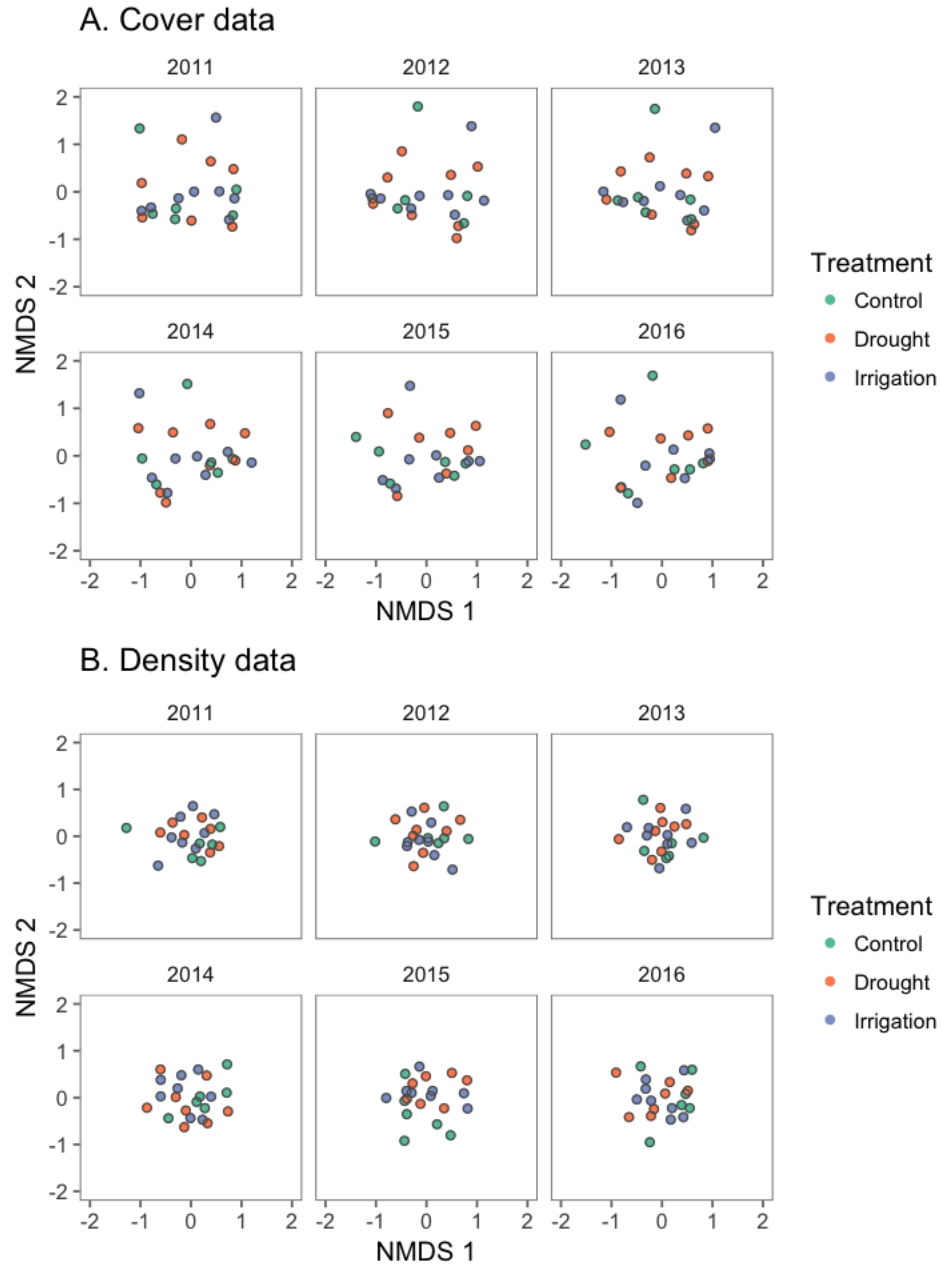
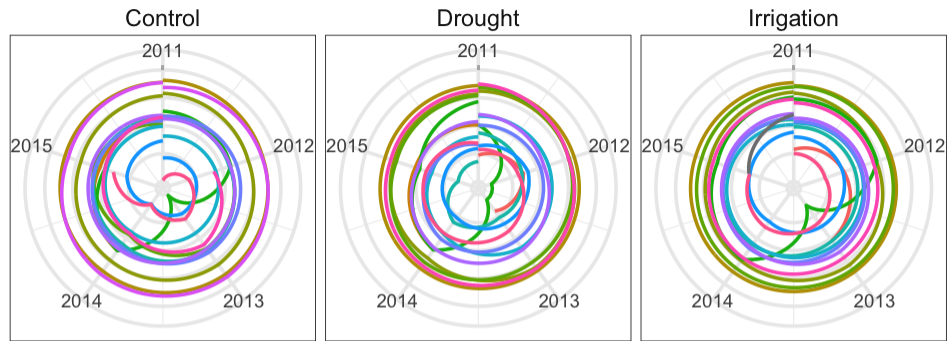


Figure 4: Nonmetric multidimensional scaling scores representing plant communities in each plot, colored by treatment. (A) NMDS results using basal cover data; (B) NMDS results using individual density data. 2011 is a pre-treatment year.

A. All species



B. Dominant species

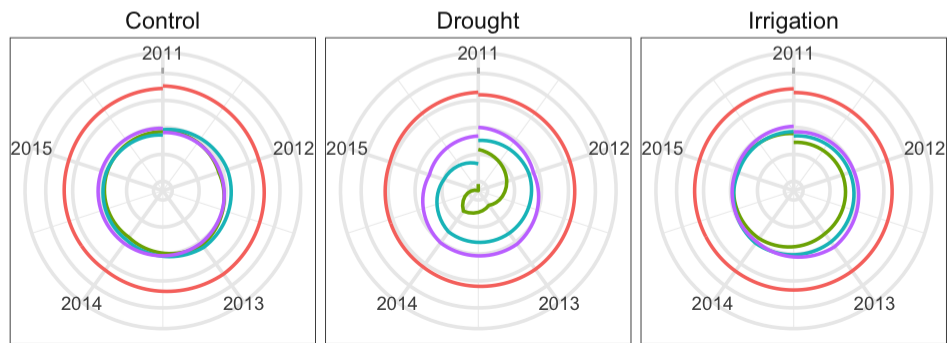


Figure 5: Rank clocks of average species' basal cover by treatment. (A) All species. (B) Dominant species. Cover is log-transformed to improve visualization of species with low cover.

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