Consistent ecosystem functional response during 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 in water limited grasslands. 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 suprisingly 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.

1 INTRODUCTION

Water availability is a strong driver of aboveground net primary productivity (ANPP) in grassland ecosystems. Mean annual precipitation (MAP) is strongly correlated with ANPP across sites (Huxman et al., 2004), and, in water-limited ecosystems, interannual variation in MAP is also correlated with interannual variation in ANPP (Hsu et al., 2012). These relationships suggest that chronic alterations in levels of precipitation, associated with global climate change, will impact ANPP.

At a given site, the functional response of 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 show a linear soil moisture-ANPP relationship, but that relationship could potentially saturate if soil moisture is pushed far beyond typical levels. Saturating relationships are actually common (Hsu et al., 2012), perhaps because other resources, like nitrogen, become more limiting in wet years than dry years. Knowing the curvature of the soil moisture-ANPP relationship is critical for understanding how ecosystems will respond to chronic alterations in water availability.

Another problem with relying on historical ecoystem 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 producting 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 annual net primary productivity (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 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, 2015; 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 (Figure 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' indentities 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 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 (50% decrease/increase) 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 underly 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 intercepts, random slopes 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).

2 METHODS

2.1 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^{-1} and mean monthly temperature ranged from -5.2°C in January to 21.8°C in July.

2.2 Precipitation Experiment

Between 1926 and 1932, range scientists at the USSES established 26 permanent 1 m^2 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 exclosure. 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 m^2 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.

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 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 two sources: yearly census maps for each plot made using a pantograph (Hill, 1920) and yearly counts of annual species in each plot. The maps record the spatial location of all individuals in the plot and the basal cover of each individual with cover greater than 1 cm. Using those annual maps, we aggregated over individuals to calculate total basal cover for each species in each plot. 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, but comes with the limitation that all species are weighted equally. Nonetheless, this scaling approach allows a comprehensive view of community composition dynamics through time.

2.4 Data Analysis

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

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

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

$$y_{i(j(k(t)))} \sim \text{Normal}\left(\mu_{i(j(k(t)))}, \sigma_k^2\right), \tag{2}$$

where $\mu_{i(j(k))}$ is the deterministic prediction from the regression model for observation i for plot j associated with treatment k in year t, $\beta_{0,j(k)}$ is the intercept for plot j associated with treatment k, $\beta_{1,j(k)}$ is the slope term for the effect of soil moisture for plot j associated with treatment k, γ_t is the intercept offset for year t, and σ_k^2 is the process variance for treatment k. Data include the standardized log(ANPP) observations $\left(y_{i(j(k(t)))}\right)$ and soil moisture (x_i). Although we include observation subscript i on the xs, observations within a treatment-year all share the same soil moisture values.

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

$$\boldsymbol{\beta}_{j(k)} \sim \text{MVN}\left(\boldsymbol{\beta}_k, \boldsymbol{\Sigma}(k)\right), \tag{3}$$

$$\boldsymbol{\beta}_k \sim \text{MVN}\left(\boldsymbol{\beta}, \boldsymbol{\Sigma}\right), \tag{4}$$

$$\boldsymbol{\beta} \sim \text{Normal}\left(0, 1\right), \tag{5}$$

where $\boldsymbol{\beta}_{j(k)}$ is the vector of regression coefficients (intercept and slope) for plot j associated with treatment k, $\boldsymbol{\beta}_k$ is the vector of coefficients for each treatment, and $\boldsymbol{\beta}$ is the vector of overall coefficients. The plot- and treatment-level coefficients are drawn from multivariate normal distributions with covariance matrix $\boldsymbol{\Sigma}$. For the plot-level coefficients, each treatment has its own variance-covariance matrix (i.e., $\boldsymbol{\Sigma}(k)$). The overall coefficients are drawn from a normal prior with mean 0 and standard deviation 1. The random year effects ($\boldsymbol{\gamma}$) are drawn from a normal prior with mean 0 and standard deviation σ_{year}, which was drawn from a weibull distribution. A full description of model is in Appendix 2.

We fit the model using a Bayesian approach, obtaining posterior estimates of all unkowns via the No-U-Turn Hamiltonian Monte Carlo sampler in Stan (Stan Development Team, 2016b). We used the R package 'rstan' (Stan Development Team, 2016a) 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$^{\text{th}}$ 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. Because we standardized species' abundances, some values were negative, which is not allowed for calculating Bray-Curtis distances. We simply added '2' to each abundance value to ensure all values were greater than zero. We plotted the first two axes of NMDS scores to see if community composition overlapped, or not, among treatments in each year. We used the 'metaMDS()' function in the R package 'vegan' (Oksanen, 2016) to calculate Bray-Curtis distances and then to run the NMDS analysis. We used the 'vegan::adonis()' function (Oksanen, 2016) to perform permutational multivariate analysis of variance to test whether treatment plots formed distinct groupings. To test whether treatment plots were equally dispersed, or not, we used the 'vegan::betadisper' function (Oksanen, 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 2.

3 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^{-2} in 2014 to a maximum of 237.1 g m^{-2} 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.

Cumulative growing season soil moisture had a positive effect on ANPP (mean of β_1 = 0.43; 80% BCI = -0.05, 0.88; 95% BCI = -0.36, 1.15) (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 conrol plot is greater than ANPP in a drought plot was 0.71, and the probability that ANPP in a control plot is lower than in an irrigation plot was 0.41. 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 there was no directional trend in the yearly treatment effects estimated from the ANPP-Treatment model (Fig. 3).

Community composition was similar among treatments. In no year did community composition among treatments not overlap, and they were equally dispersed in all years (Table 1; Fig. 4). Likewise, community composition was remarkably stable over time, with no evidence of divergence among treatments (Table 1; Fig. 4). Species' abundances and ranks showed little deviation over the five-year experiment, regardless of treatment (Fig. 5).

4 DISCUSSION

Ecosystem response to chronic resource alteration is expected to follow a temporal trend. Initially, ecosystem response will be modest and reflect the physiological responses of constituent species. Over longer time periods, species reordering will cause greater responses as species better able to take advantage of, or cope with, new resource levels become more abundant. This temporal trend is formalized by the 'Hierarchical Response Framework' (HRF, Smith et al., 2009), and has been empirically supported (Knapp et al., 2012; Wilcox et al., 2016). A lingering question is not whether the HRF is a reasonable model of ecosystem dynamics, but rather how the time scales of ecosystem response and community change differ among ecosystems. Indeed, 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). To add to this growing body of knowledge, we performed a precipitation manipulation experiment in a sagebrush steppe ecosystem.

Surprisingly, ANPP was not sensitive to either drought or irrigation treatments, whether in the context of growing season precipitation (Fig. 2) or in the context of year since the experiment began (Fig. 3). This is surprising because grasslands generally, and sagebrush steppe specifically, are considered water-limited systems. Thus, our expectation was that ANPP would be tightly linked to soil water availability. ANPP was slightly lower in drought plots and slightly higher in irrigation plots, but these differences were not statistically important.

In the absence of community composition data, an obvious hypothesis to explain the lack of ANPP response is that species reordered rapidly. In so doing, newly abundant species could compensate for the loss of ecosystem functioning of previously abundant species. We did not find this to be the case, as specie composition was remarkably stable over the course of the experiment (Fig. 3).

In combination, the lack of ecosystem and community response to drought or irrigation shows that this sagebrush steppe ecosystem is resistant to chronic alterations in water availability. There are three possible explanations for the resistance we found. First, it could be that our experiment simply was not long enough to induce responses. This may be true for community responses, which can take decades

(Wilcox et al., 2016), but the response of grassland ANPP to water manipulations is typically immediate (e.g., Hoover et al., 2014).

Second, 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 give our sites 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 neccesary 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. 1A). The irrigation treatment may have been too small, however.

Third, the ecosystem and community resistance to drought and deluge we observed could be a real phenomenon in this system.

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7 TABLES

Table 1. Results from statistical tests for clustering and dispersion of community composition among precipitation treatments. 'adonis' tests whether treatments form unique clusters in multidimensial 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	0.45
2011	betadisper	21	2	2.23	0.14
2012	adonis	22	2	1.10	0.29
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	0.58
2014	betadisper	22	2	0.35	0.71
2015	adonis	21	2	1.05	0.37
2015	betadisper	21	2	3.01	0.07
2016	adonis	21	2	1.07	0.35
2016	betadisper	21	2	0.50	0.62

8 FIGURES

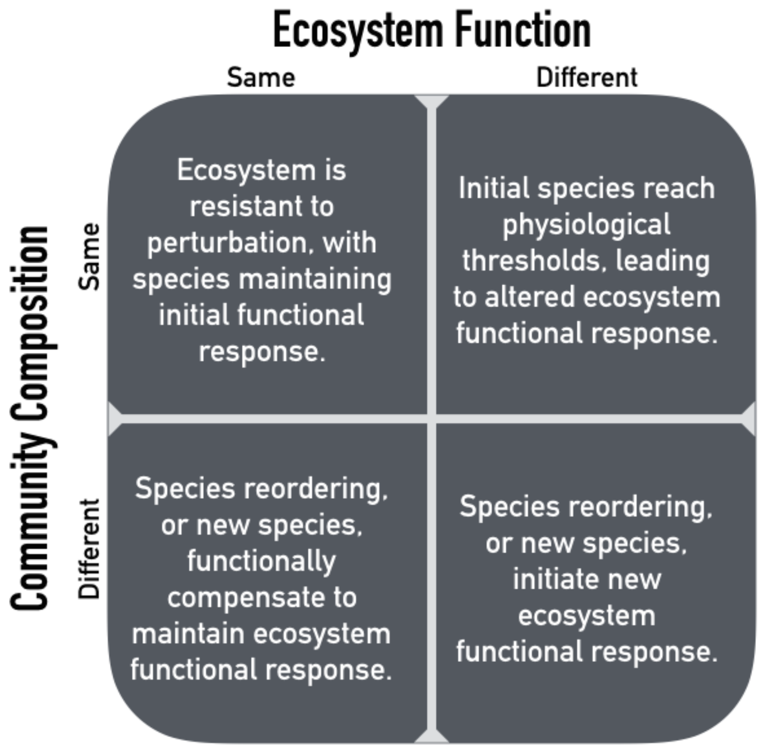

Figure 1. Possible outcomes of chronic resource alteration.

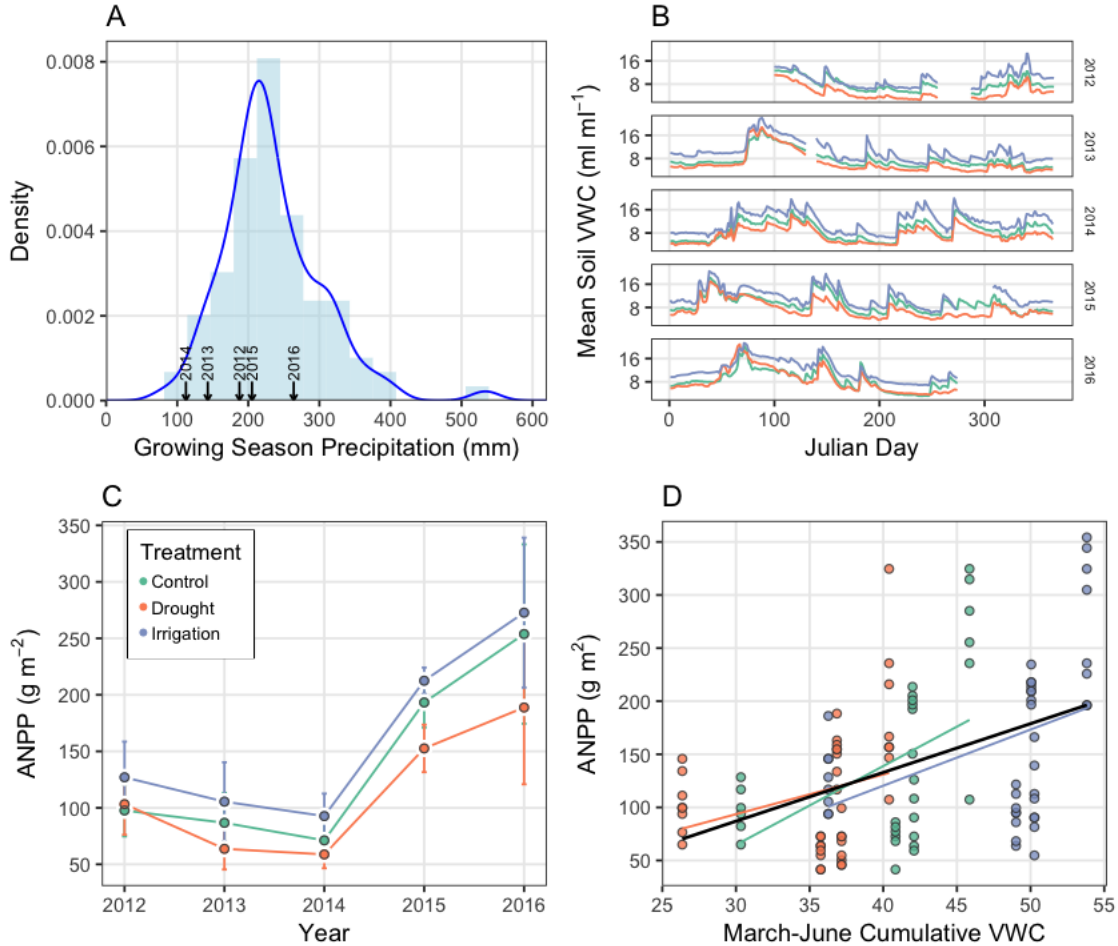

Figure 2. (A) Probability density of historical precipitation from 1926-2016, with the years of the experiment shown with arrows on the *x*-axis. (B) Observed soil volumetric water content (VWC) over the course of the experiment. (C) Mean (points) ANPP and its standard deviation (error bars) for each year of the experiment. (D) Scatterplot of ANPP versus growing season precipitation. Colored regression lines are independently-fit linear models for each treatment with no random effects structure; dark black regression line is a linear regression through all the point with no random effects structure. Our analysis seeks to find if the data supports a model with different intercepts and/or slopes for each treatment, while also accounting for nonindependence of samples within plots across years. Color mapping for panels B-D is shown in the legend for panel C.

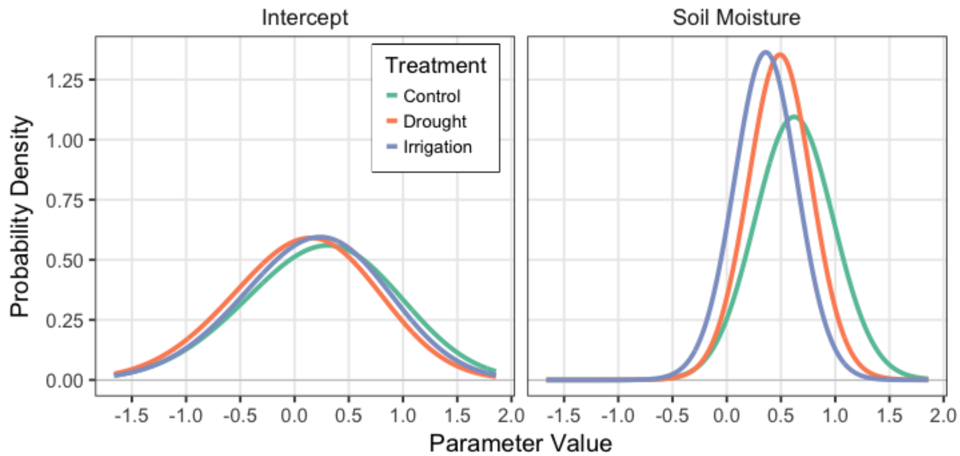

Figure 3. Posterior distributions of treatment-level parameters ('Intercept' and the effect of 'Soil Moisture'). Kernel bandwidths of posterior densities were adjusted by a factor of 5 for visual clarity.

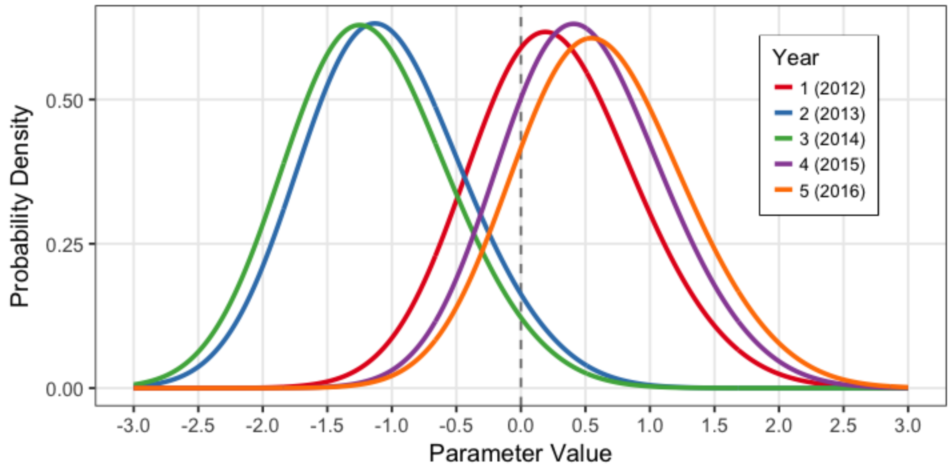

Figure 4. Posterior distributions of random year effects (intercept offsets). Kernel bandwidths of posterior densities were adjusted by a factor of 5 for visual clarity.

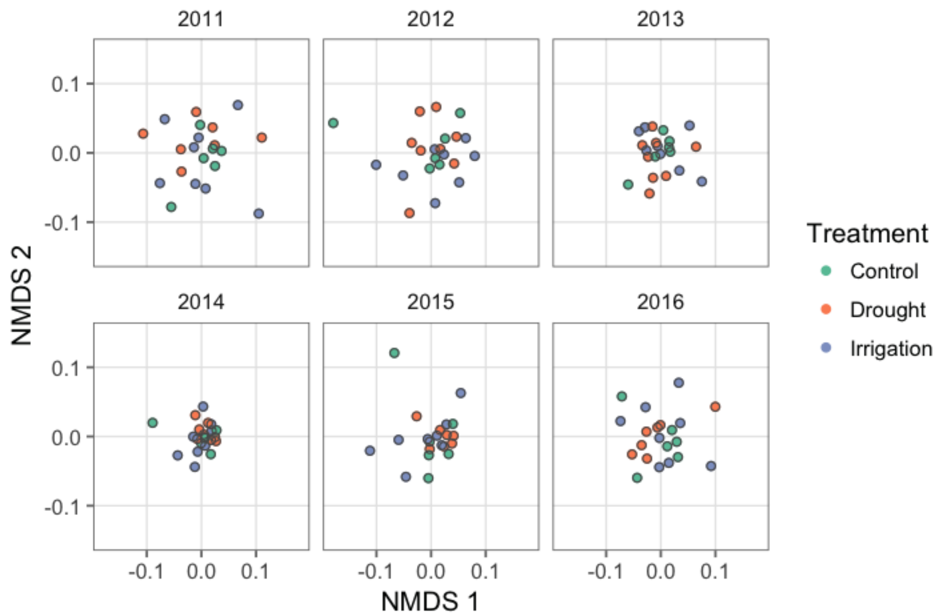

Figure 5. Nonmetric multidimensional scaling scores representing plant communities in each plot, colored by treatment.

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