

Can historical data predict population responses to climate change experiments?

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¹ **Abstract**

² Climate is an important driver of population dynamics and annual variation in demographic rates
³ often correlate with variation in weather. However, the predictive potential of such correlations is
⁴ largely unknown. We tested how well population models fit using long-term observational could pre-
⁵ dict the responses of four dominant plant species in a sagebrush steppe to a drought and irrigation
⁶ experiment.

⁷ We used rainout shelters and automatic sprinklers to manipulate the soil moisture in sixteen
⁸ plots established at the same field site where long-term observational data was collected. We report
⁹ how the growth, survival and recruitment of each species responded to the experimental drought
¹⁰ and irrigation treatments after five years. We then attempted to predict these treatment responses
¹¹ using two models fit to the observational data collected prior to the experiment: a no climate
¹² model that only included the effects of plant size and competition on plant performance in each
¹³ plot in each year, and a climate model that also included the effects of three seasonal soil moisture
¹⁴ variables. We compared predictions made by the no climate and climate models to the actual
¹⁵ experimental responses. We also generated one-step-ahead predictions of population size in each
¹⁶ experimental plot using individual based population parameterized with the vital rate estimates
¹⁷ from the climate and no climate models.

¹⁸ Over the course of the experiment, average cover of the perennial grasses, *Hesperostipa*
¹⁹ *comata* and *Pseudoroegneria spicata* declined significantly in the drought treatment. At the level
²⁰ of individual vital rates, experimental drought reduced the survival of *Hesperostipa comata* and
²¹ *P. spicata* and the growth of the grass *Poa secunda*. In contrast, drought increased the growth of
²² the shrub *A. tripartita*. The climate model made better predictions of the experimental responses
²³ than the no climate model in six out of twelve cases. Across all species and vital rates, there was
²⁴ a strong positive correlation between the observed responses to the treatments and the responses
²⁵ predicted by the climate model. At the population-level, the climate model predicted changes in
²⁶ species cover more accurately than the no climate model for *P. secunda* and *P. spicata*.

²⁷ Observational climate data held valuable information for predicting species' responses to
²⁸ a climate change experiment in this ecosystem. Treatment responses often matched the direction
²⁹ of predicted responses even when the effects were not significant. We were better able to predict

30 species' responses to the drought treatment than to the control and irrigation treatments, suggesting
31 that soil moisture is an important factor for predicting the population dynamics of these species
32 but only when water is truly limiting.

33 Introduction

34 Climate is one of the most powerful drivers of changes in species abundance across space and time
35 (Post and Forchhammer, 2002; Davis and Shaw, 2001; Walther et al., 2002). The effects of climate
36 on populations and ecosystems are most apparent at the largest scales: climate determines the
37 distribution of ecosystems (Whittaker, 1975), treelines (Kerner, 2012) and the range limits of
38 many species (Parmesan and Yohe, 2003; Davis and Shaw, 2001). Understanding and predicting
39 the effects of climate on populations is an increasingly important goal if we are to anticipate the
40 effects of climate change on earth's ecosystems (Tredennick et al., 2016; Petchey et al., 2015; Ehrlin
41 et al., 2016; Teller et al., 2016).

42 Ecologists often resort to one of two methods for predicting the effects of future climate
43 change on populations and communities: they may use experiments to manipulate aspects of
44 climate directly and observe the response of populations (Elmendorf et al., 2015; Knapp et al., 2016;
45 Compagnoni and Adler, 2014); or they may use long term observational data on species performance
46 and abundance collected over many years and relate this to ambient annual variation in climate
47 (Koons et al., 2012; Lunn et al., 2016; Dalgleish et al., 2010; Jenouvrier et al., 2009). The strength of
48 the experimental approach is in the stronger inference that comes from manipulating some aspects
49 of climate while controlling for other factors; for instance, knowing that loss of snow cover, and not
50 necessarily changes in soil temperature or moisture are factors causing a species performance to
51 change with warming (Compagnoni and Adler, 2014). It also allows for the creation of conditions
52 that may be more extreme than those observed historically Knapp et al. (2016) but are possible
53 in the future. However, it is often expensive to control climate at even the smallest scales, and
54 larger scale climate manipulation is often impossible. Moreover, experimental manipulation can
55 come with artifacts that may make them less than ideal models for understanding and predicting
56 the effects of future variation in climate (Wolkovich et al., 2012).

57 The use of observational data to predict the effects of climate variation on populations
58 has its own advantages and disadvantages. One important advantage is cost: analyses of already

59 existing long-term ecological data and ever increasingly detailed climate data are cheaper than
60 experiments. Observational studies may also be the only way to study the effects of climate on
61 large and or migratory species, for which it would be difficult to manipulate climate (Koons et al.,
62 2012; Jenouvrier et al., 2009; Aubry et al., 2013). The principal disadvantage is the reliance
63 on essentially correlative relationships between species performance and climate to predict future
64 species' responses. First, many years of data are needed to reliably detect climate effects, especially
65 when annual variation in demographic rates is high (Teller et al., 2016; Gerber et al., 2015). (Teller
66 et al., 2016) estimate that even cutting edge statistical approaches for fitting relationships between
67 climate and species performance require at least 20-25 years of independent climate observations
68 before they perform well. Moreover, even strong correlations between species performance and the
69 climate covariates we choose to include in our models may not reflect direct causation, leading to
70 failures when predicting future, out of sample performance (Hilborn, 2016).

71 The extrapolation of climate-demography correlations presents another potential problem.
72 In many systems, future precipitation and temperature will fall outside the range of historical
73 variation. If species performance responds non-linearly to these drivers, fitting linear models for
74 species responses to climate may produce larger errors when future conditions are outside the range
75 of observed variation (Doak and Morris, 2010). In addition, climate change will not only alter
76 average weather, but is also likely to increase the variance in precipitation and the frequency of
77 extreme events, which will have their own consequences independent of changes in means (Gherardi
78 and Sala, 2015; Jentsch et al., 2007). Any models based on observations drawn from the historical
79 range of variation will therefore be extrapolating beyond both the range of observed averages and
80 variances when used to predict the future (Williams and Jackson, 2007).

81 Here, we combine the strengths of experimental and observational approaches by testing
82 the ability of models fit to historical data to predict the effects of experimental climate manipu-
83 lations that generate extreme conditions. A demonstration that the observational approach can
84 skillfully predict experimental responses would provide strong confirmation that observed climate-
85 demography correlations are not spurious and will hold even in novel conditions in the future Adler
86 et al. (2013). (Adler et al., 2013) showed that population models based on observed correlations
87 between plant population growth rates and precipitation did have some predictive power in de-
88 scribing species response to a short-term climate manipulation. Three species showed responses

89 to experimentally imposed drought and irrigation that were well predicted by population models
90 fitted to historical observations. However, the responses of another three species, were not well
91 predicted by historical observations.

92 Among plant populations, interannual variation in precipitation and or soil moisture often
93 drives variation in net primary productivity (Knapp and Smith, 2001; Hsu and Adler, 2014), the
94 annual growth rates of the woody tissue in trees and shrubs ((Yang et al., 2014),(Srur and Villalba,
95 2009; Franklin, 2013)), and the germination and reproductive output of annuals (Venable, 2007).
96 Despite clear signs that precipitation shold be important for plant populations, there have been
97 relatively few studies that clearly link observed variation in precipitation to species performance in
98 population models (Ehrln et al., 2016).

99 The sagebrush steppe plant community at the US Sheep Experiment Station near Dubois,
100 Idaho offers an ideal opportunity to test whether the climate effects in plant populations models
101 derived from observational data can also be used to predict species responses to controlled precip-
102 itation experiments. The demography of three perennial bunchgrasses and a shrub species at the
103 USSES have been described in detail in seven different studies since 2010, several of which report
104 significant effects of seasonal precipitation on the vital rates and overall population growth rates of
105 these species ((Adler et al., 2010, 2012, 2009, 2016; Chu et al., 2016; Chu and Adler, 2015; Dalgleish
106 et al., 2010)).

107 In this study, we report how the four dominant plant species at the USSES respond to a
108 five year drought and irrigation experiment and use the results to address two research questions:
109 first, how much do the growth, recruitment and survival of our target species differ between the
110 precipitation manipulation treatments? Significant experimental effects on species vital rates imply
111 that future changes in precipitation will impact populations. Second, can we predict each species'
112 response to the experimental conditions based on how they respond to natural climate variation in
113 the observational data? If models based on observational data can predict the response of species
114 to this experiment we will gain confidence in using long-term population monitoring data to predict
115 species responses to future climate change.

¹¹⁶ **Methods**

¹¹⁷ **Study site and data set description**

¹¹⁸ The U.S. Sheep Experiment Station (USSES) is located at Dubois, Idaho (44.2°N, 112.1°W), 1500
¹¹⁹ m above sea level. During the period of data collection (1926–2016), mean annual precipitation
¹²⁰ was 270 mm and mean temperatures ranged from -8°C (January) to 21°C (July). The vegetation
¹²¹ is dominated by a shrub, *Artemisia tripartita*, and three perennial C3 grasses: *Pseudoroegneria*
¹²² *spicata*, *Hesperostipa comata*, and *Poa secunda*. These dominant species account for over 70% of
¹²³ basal cover and 60% of canopy cover at this site.

¹²⁴ Scientists at the USSES established 26 1-m² quadrats between 1926 and 1932. Eighteen
¹²⁵ quadrats were distributed among four ungrazed exclosures, and eight were distributed in two pad-
¹²⁶ docks grazed at medium intensity spring through fall. All quadrats were located on similar topog-
¹²⁷ raphy and soils. In most years until 1957, all individual plants in each quadrat were mapped using
¹²⁸ a pantograph (Blaisdell, 1958). The historical data set is public and available online (Zachmann
¹²⁹ et al., 2010). In 2007, we located 14 of the original quadrats, all of which are inside permanent live-
¹³⁰ stock exclosures, and resumed annual mapped censusing using the traditional pantograph method.
¹³¹ Daily temperature and precipitation has been monitored throughout this period at a climate sta-
¹³² tion located at the USSES headquarters (station id: GHCND:USC00102707) which located within
¹³³ 2 km of the research plots. We downloaded daily and monthly tmin, tmax, and precipitation data
¹³⁴ from the National Climate Data Centers online database.

¹³⁵ We extracted data on survival, growth, and recruitment from the mapped quadrats based
¹³⁶ on plants' spatial locations. Our approach tracks genets representing individual plants. For the
¹³⁷ shrub, each genet is associated with the basal position of a stem. For the bunchgrasses, each genet
¹³⁸ represents a spatially distinct polygon in the mapped quadrat. These genets may fragment and/or
¹³⁹ coalesce over time. Each mapped polygon is classified as a surviving genet or a new recruit based
¹⁴⁰ on its spatial location relative to genets present in previous years (Lauenroth and Adler, 2008). We
¹⁴¹ modeled vital rates using data from 21 year-to-year transitions between 1929 and 1957, and four
¹⁴² year-to-year transitions from 2007 to 2011.

¹⁴³ **Precipitation experiment**

¹⁴⁴ In spring 2011, we selected locations for an additional 16 quadrats for the precipitation experiment.
¹⁴⁵ We located these in a large enclosure containing six of the historical permanent quadrats. We
¹⁴⁶ avoided plots falling on hill slopes, areas with greater than 20% bare rock, or with over 10% cover
¹⁴⁷ of the woody shrubs *Purshia tridentata* or *Amelanchier utahensis*. New plots were established
¹⁴⁸ in pairs, and one plot per pair was randomly assigned to either the precipitation reduction or
¹⁴⁹ the precipitation addition treatment. We mapped the quadrats in June, 2011 and then built the
¹⁵⁰ rainfall shelters and set-up the irrigation systems in the fall of 2011. We used a rain-out shelter and
¹⁵¹ automatic irrigation design described in (Gherardi and Sala, 2013). Each rain-out shelter covered
¹⁵² an area of 2.5 by 2 m and consisted of transparent acrylic shingles held up 1.5 to 1 m over the plot
¹⁵³ to channel 50% of incoming rainfall off of the plot and into 75 l reservoirs. The collected water
¹⁵⁴ was pumped out of reservoirs and sprayed onto paired irrigation treatment plots. Pumping was
¹⁵⁵ initiated automatically with float switches that were triggered when water levels in the reservoirs
¹⁵⁶ were approximately 20 l, or equivalently irrigation was triggered once for every 6 mm of rainfall
¹⁵⁷ collected. We disconnected the irrigation pumps in late fall each year and re-connected them in
¹⁵⁸ April. The drought shelters remained in place throughout the year.

¹⁵⁹ We monitored soil moisture and air temperature in four of the precipitation experiment plot
¹⁶⁰ pairs using Decagon Devices (Pulman Washington) 5TM and EC-5 soil moisture sensors and 5TE
¹⁶¹ temperature sensors. We installed two soil moisture sensors in each monitored plot at 5 cm and
¹⁶² two at 25 cm deep in the soil. Air temperature was measured underneath the roofing of the shelter
¹⁶³ at 30 cm above ground. For each pair of manipulated plots, we also installed sensors in a nearby
¹⁶⁴ area to measure ambient rainfall and temperature. Data were logged automatically every four
¹⁶⁵ hours. We augmented automatic monitoring of the climate in these plots with direct measurements
¹⁶⁶ of soil moisture with a handheld EC-5 soil moisture sensor at six points around all 16 plots on
¹⁶⁷ 6/6/2012, 4/29/2015, 5/7/2015, 6/9/2015 and 5/10/2016. We analyzed these spot measurements
¹⁶⁸ for significant treatment effects on soil moisture using a linear mixed effects model with the *lmer*
¹⁶⁹ package in *R*, with plot, plot group, and date as random effects in the model ((Bates et al., 2015)).

¹⁷⁰ We conducted a simple statistical to determine the net effect of the experimental treatments
¹⁷¹ on cover in the experiment. First we calculated the log change in cover for each of the four focal

172 species in each quadrat from from the start of the experiment in spring prior to manipulation, to
173 the last year of the experiment. Log change in cover was defined as , $\log(Cover_{2016}/Cover_{2011})$
174 where $Cover_{2016}$ is the cover of each species in 2011 and $Cover_{2015}$ is cover in 2011. We tested for
175 the effect of precipitation treatment on this measure with a linear model in *R*.

176 **Soil moisture modeling**

177 We expected that our precipitation manipulation experiment would affect plants by altering avail-
178 able soil moisture during the growing season. Because we do not have direct soil moisture measures
179 for each year of observed plant cover in the historical record, we used the SOILWAT soil moisture
180 model to estimate daily soil moisture at the USSES from 1925 to the present (Sala et al., 1992). We
181 used an enhanced version of SOILWAT that has recently been developed for use in semi-arid shrub-
182 land ecosystems (Bradford et al., 2014). SOILWAT uses daily weather data, ecosystem specific
183 vegetation properties and site specific soil properties to estimate water balance processes. SOIL-
184 WAT specifically estimates rainfall interception by vegetation, evaporation of intercepted water,
185 snow melt and snow redistribution, infiltration into the soil, percolation through the soil, bare-soil
186 evaporation, transpiration from each soil layer, and drainage. We parameterized SOILWAT with
187 the generic sagebrush steppe vegetation parameters and site specific soil texture and bulk density
188 data. We used daily weather data collected at the USSES from 1925 until the present as weather
189 forcing data for the SOILWAT predictions.

190 We averaged daily soil moisture predictions from SOILWAT from upper 40 cm of soil and
191 then averaged these seasonally to serve as the covariates in the vital rate regressions for each species.
192 Because we did not monitor soil moisture directly in all control, drought and irrigation plots, we
193 used a model to describe the average treatment effects on soil moisture during the course of the
194 experiment. To do this we first averaged observed soil moisture data by date and plot and then
195 standardized these by the mean and standard deviation of the control soil moisture conditions
196 observed within each plot group. We then found the difference between the soil moisture in the
197 treated plots and the ambient conditions. We then modeled these treatment effects as a function of
198 season and whether a day was rainy or dry. We expected that our drought and irrigation treatments
199 might be more effective during rainy weather than during dry weather. Rainy days were defined
200 as any days when any precipitation was recorded and average temperatures were above 3 degrees

201 C. The day immediately following rainfall was also classified as rainy. We fit this model using
202 the *lmer* package in *R* with random effects for plot group and date (Bates et al., 2015). We then
203 used this model to predict the treatment effects on soil moisture for the entire study period from
204 the ambient soil moisture values predicted from the SOILWAT model described above. These
205 adjusted soil moisture values reflected the average season and rainfall dependent effects of the
206 experimental treatments on soil moisture and could be used as covariates for predicting the effects
207 of our manipulation on each species demographic rates.

208 **Overview of the analysis**

209 Our analysis consists of two separate datasets and three different categories of vital rate models.
210 We refer to the first dataset as the observational data. It consists of all the historical data collected
211 from 1925 to 1957 as well as the contemporary data collected from the same plots from 2007 to
212 2010. These data record the response of plants in each plot to the ambient climate variation. We
213 refer to the second dataset as the experimental data. It consists of the data collected from 2011 to
214 2016 from the 16 new experimentally manipulated plots, as well as from 14 of the original historical
215 plots which serve as ambient climate controls.

216 In order describe the effects of the experimental treatments on each vital rate, we fit "treat-
217 ment" models. The treatment models included parameters representing the effects of the drought
218 and irrigation treatments on each vital rate. We fit these models to using all the experimental and
219 all the observational data. We combined the datasets because we wanted to focus our predictions
220 on the effects of the experimental treatments on the vital rates, rather than any differences between
221 the historical and contemporary periods in the effects of crowding and plant size on the vital rates.

222 Next, in order to test how well we could predict the responses in the experimental plots,
223 we fit two classes of models to the observational dataset only. The "no climate" models include
224 parameters for the effects of competition on each vital rate and the size dependence of survival and
225 growth but they do not include climate or treatment effects. The "climate" models include the
226 effects of annual variation in soil moisture on each vital rate. The no climate model provides us a
227 baseline by which to measure the accuracy of predictions from the climate model. Because much of
228 the variation in growth, survival and recruitment in this system can be explained by plant size and
229 competition, we expect that these two models will make similar predictions for individual plant

230 performance in the experiment. However, if the climate model makes more accurate predictions
 231 than the no climate model, this indicates that the climate parameters it includes contain useful
 232 information for prediction. Note that because these models are fit using only the observation
 233 dataset, when we use these models to predict experimental responses we are generating true out-
 234 of-sample predictions.

235 **Statistical models of vital rates**

236 All three categories of models described above follow the same basic structure and differ only in
 237 how they treat climate and treatment effects and (Adler et al., 2010; Chu and Adler, 2015). We
 238 model the survival probability of an individual genet as a function of genet size, the neighborhood-
 239 scale crowding experienced by the genet from both conspecific and heterospecific genets, temporal
 240 variation among years, and permanent spatial variation among groups of quadrats ('group'; here
 241 means a set of nearby quadrats located within one pasture or grazing exclosure). In this analysis
 242 we only include crowding from the four main focal species.

243 Formally, we modeled the survival probability, S , of genet i in species j , group g , and from
 244 time t to $t + 1$ as

$$\text{logit}(S_{ijg,t}) = \varphi_{jg}^S + \gamma_{j,t}^S + \beta_{j,t}^S u_{ij,t} + \langle \boldsymbol{\omega}_{j,t}^S, \mathbf{W}_{ij,t} \rangle \quad (1)$$

245 where φ is the spatial group dependent intercept, γ is a year-effect, β is year-dependent coefficient
 246 that represents the effect of log genet size, u , on survival in year t . $\boldsymbol{\omega}$ is a vector of interaction
 247 coefficients which determine the impact of crowding, \mathbf{W} , by each species on the focal species. The
 248 vector \mathbf{W} includes crowding from the four dominant species, *A. tripartita*, *P. spicata*, *H. comata*,
 249 and *Poa secunda*. $\langle \mathbf{x}, \mathbf{y} \rangle$ denotes the inner product of vectors \mathbf{x} and \mathbf{y} , calculated as `sum(x*y)` in
 250 R. This model is the no climate model for survival.

251 In the treatment model, a new term is added to the above model, $\mathbf{T}\chi_j^S$ where χ is a vector
 252 of treatment effect coefficients for each experimental treatment level h on the survival rate, and \mathbf{T}
 253 is a design matrix indicating the treatment level of each observation in the data. The design matrix
 254 also includes terms for the interaction between plant size u and the treatment effects which allow
 255 the effect of each treatment to vary with plant size.

256 In the climate model, the above term is replaced with $\mathbf{C}\xi_j^S$, where ξ gives a vector of
 257 coefficients describing the effects of a set of soil moisture covariates \mathbf{C} in treatment h and year t

258 on the survival rate of species j . \mathbf{C} can include interaction effects between plant size, u , and the
 259 soil moisture covariates allowing the effects of soil moisture to vary with plant size.

260 Our growth model has a similar structure. The change in genet size from time t to $t + 1$,
 261 conditional on survival, is given by:

$$u_{ijg,t+1} = \varphi_{jg}^G + \gamma_{j,t}^G + \chi_{jh}^G + \beta_{j,t}^G u_{ij,t} + \langle \boldsymbol{\omega}_{j,t}^G, \mathbf{W}_{ij,t} \rangle + \varepsilon_{ij,t}^G. \quad (2)$$

262 As in the survival regression above, parameters describing the treatment effects on growth
 263 are added in the treatment model, $\mathbf{T}\chi_j^G$, where χ is a treatment effect describing the effect of
 264 experimental treatment h on growth, including treatment by size interactions.

265 Similarly, in the climate model, the above term is replaced with $\mathbf{C}\xi_j^G$, where ξ is a vector
 266 of coefficients describing the effects of soil moisture covariates in the matrix \mathbf{C} for treatment h and
 267 year t on growth of species j . Again this can include interactions between soil moisture and plant
 268 size u .

269 Although the main focus of the current analysis the effects of soil moisture, we also modeled
 270 the effects of inter- and intra-specific competition in our vital rate models. We model the crowding
 271 experienced by a focal genet as a function of the distance to and size of neighbor genets. These
 272 effects are well described in previous work (Teller et al., 2016; Adler et al., 2016). Briefly, we model
 273 the crowding experienced by genet i of species j from neighbors of species m as the sum of neighbor
 274 areas across a set of concentric annuli, k , centered at the plant,

$$w_{ijm,k} = F_{jm}(d_k)A_{i,k} \quad (3)$$

275 where F_{jm} is the competition kernel (described below) for effects of species m on species j , d_k is
 276 the average of the inner and outer radii of annulus k , and $A_{im,k}$ is the total area of genets of species
 277 m in annulus k around genet i . The total crowding on genet i exerted by species m is

$$W_{ijm} = \sum_k w_{ijm,k}. \quad (4)$$

278 Note that W_{ijj} gives intraspecific crowding. The W 's are then the components of the \mathbf{W} vectors
 279 introduced as covariates in the survival (1) and growth (2) regressions.

280 We assume that competition kernels $F_{jm}(d)$ are non-negative and decreasing, so that distant
 281 plants have less effect than close plants. Otherwise, we let the data dictate the shape of the kernel
 282 by fitting a spline model using the methods of Teller et al. (2016). We used data from all historical
 283 plots and contemporary control-treatment plots to estimate the competition kernels and these are
 284 described in more detail in (Adler et al., 2016).

285 Once we had estimated the competitions kernels, we used them to calculate the values of \mathbf{W}
 286 for each individual, and fit the full survival and growth regressions, which include the interspecific
 287 interaction coefficients, $\boldsymbol{\omega}$. All genets in a quadrat were included in calculating W , but plants
 288 located within 5 cm of quadrat edges were not used in fitting.

289 We model recruitment at the quadrat level rather than at the individual genet level because
 290 the mapped data do not allow us to determine which recruits were produced by which potential
 291 parent plants. We assume that the number of individuals, y , of species j recruiting at time $t + 1$ in
 292 the location q follows a negative binomial distribution:

$$y_{jq,t+1} = NegBin(\lambda_{jq,t+1}, \theta) \quad (5)$$

293 where λ is the mean intensity and θ is the size parameter. In turn, λ depends on the composition
 294 of the quadrat in the previous year:

$$\lambda_{jq,t+1} = C'_{jq,t} \exp \left(\varphi_{jg}^R + \gamma_{j,t}^R + \langle \boldsymbol{\omega}^R, \sqrt{\mathbf{C}'_{q,t}} \rangle \right) \quad (6)$$

295 where the superscript R refers to Recruitment, $C'_{jq,t}$ is the ‘effective cover’ (cm^2) of species j in
 296 quadrat q at time t , φ is a group dependent intercept, γ is a random year effect, $\boldsymbol{\omega}$ is a vector of
 297 coefficients that determine the strength of intra- and interspecific density-dependence, and \mathbf{C}' is
 298 the vector of “effective” cover of each species in the community. Following previous work (Adler
 299 et al., 2010), we treated year as a random factor allowing intercepts to vary among years.

300 Because plants outside the mapped quadrat could contribute recruits to the focal quadrat or
 301 interact with plants in the focal quadrat, we estimated effective cover as a mixture of the observed
 302 cover, C , in the focal quadrat, q , and the mean cover, \bar{C} , across the spatial location, g , in which

303 the quadrat is located: $C'_{jq,t} = p_j C_{jq,t} + (1 - p_j) \bar{C}_{jq,t}$, where p is a mixing fraction between 0 and
304 1 that was estimated as part of fitting the model.

305 In the treatment model for recruitment, a new term is added to the exponential term in
306 the equation above, $\mathbf{T}\boldsymbol{\chi}_j^R$ where $\boldsymbol{\chi}$ describes the effect of each treatment level on recruitment.

307 Likewise in the climate model this term is replaced by $\mathbf{C}\boldsymbol{\xi}_j^R$ where the $\boldsymbol{\xi}$ gives a set of
308 coefficients for the year, and treatment specific soil moisture covariates in \mathbf{C} .

309 We fit all vital rate models using Hamiltonian-Markov Chain Monte Carlo (HMC)C
310 simulations in the programs STAN 10.1 and rStan (). The priors and model code are described more
311 completely in appendix A. Each model was run for 2,000 iterations and four independent chains
312 with different initial values for parameters. We discarded the initial 1,000 samples. Convergence
313 was observed graphically for all parameters, and confirmed by assessing the split \hat{R} statistic which
314 at convergence is equal to one ()�.

315 We fit the treatment models for species survival and growth with and without the size
316 by treatment interactions in the treatment effect term $\boldsymbol{\chi}$. We then judged whether including the
317 interaction terms improved model fit by comparing the Watanabe-Aikake Information Criteria
318 (WAIC) scores of each version of the model and retained the version with the lower WAIC score
319 (?). WAIC are similar to AIC scores and allow for comparison of Bayesian models. Lower WAIC
320 scores indicate a more parsimonious model. When a treatment model for survival or growth of a
321 species included a size by treatment effect in $\boldsymbol{\chi}$, we also included a size by soil moisture effect in
322 the $\boldsymbol{\xi}$ term in the climate model for that species and vital rate. This allowed us to more directly
323 compare the predictions from the climate model to the effects in the treatment model.

324 Selecting soil moisture covariates

325 After generating a time series of predicted daily soil moisture from SOILWAT, we averaged daily
326 soil moisture across spring, summer and fall seasons in each year. We considered each of the three
327 seasonal soil moisture variables at three different time periods relative to the demographic transition
328 from year t to year $t + 1$. Soil moisture in the year between t and $t + 1$ is indicated with a "1"
329 subscript. Soil moisture in the year before t is indicated with a "0" subscript. And soil moisture
330 preceding this year is indicated with a "lag" subscript. For example, for the year 2010, $spring_1$

331 indicates soil moisture in the spring of 2010, $spring_0$ indicates soil moisture during spring of 2009
332 and $spring_{lag}$ indicate soil moisture during spring 2008.

333 We wanted to avoid fitting nine soil moisture covariates (three seasons and three lags each)
334 for each species and vital rate, so we used only three soil moisture covariates per species and vital
335 rate. We selected these three by calculating the correlations of each soil moisture variable with
336 the random year effects from the no climate model fit and then selecting the three soil moisture
337 variables with the strongest correlations with these year effects. This screening technique has
338 been used in previous demographic studies at this site (Dalgleish et al., 2010) and is often used in
339 dendrochronology to screen for potential climate influence on tree-ring growth (Wang et al., 2003).
340 We felt this approach was justified because we did not make inference on these fitted parameters
341 until after we validated their ability to predict the out of sample data in the experimental plots.

342 Predicting cover from individual-based models

343 The vital rate regressions allow us to evaluate whether soil moisture and the experimental treat-
344 ments had an effect on species performance. But the population response ultimately depends on
345 the integrated effects of treatment or soil moisture on all three vital rates. To evaluate whether the
346 climate models could predict the responses of these species in the drought and irrigation experiment
347 at the overall population level we used an individual-based model (IBM) to compare observed and
348 predicted changes in population size from one year to the next.

349 To simulate changes in cover in each quadrat from year t to year $t + 1$, we initialized the
350 IBM with the observed genet sizes and locations of the four focal species observed in year t in each
351 quadrat. For every individual genet in a quadrat, we projected its size and survival probability in
352 the next year using the growth and survival models and the appropriate crowding and soil moisture
353 or treatment covariates for that year and quadrat. Likewise we projected the number of new recruits
354 in the quadrat in the next year using the recruitment model. We calculated the expected cover in
355 year $t + 1$ as the total area of new recruits, plus the sum of the predicted area of each existing plant
356 at time $t + 1$ multiplied by each plant's expected survival probability from time t to $t + 1$.

357 We generated predictions using 1000 samples from the posterior distributions of each model
358 parameter which allowed us to carry forward all of the uncertainty of the fitted vital rate models into
359 our cover predictions. Because we were interested in comparing model predictions to observations,

360 and were not interested in the effects of demographic stochasticity, we used a deterministic version
361 of the models (e.g., recruitment is the λ of (6), rather than a random draw from a negative binomial
362 distribution with a mean of λ).

363 After generating predictions for each year from the climate and no climate models, we found
364 the predicted quadrat-level changes in cover as $\log(Cover_{t+1}/Cover_t)$.

365 Quantifying predictive accuracy

366 We assessed the predictive performance of the climate and no climate by calculating the mean
367 square error (MSE) between the predicted and observed responses in the experimental data as,

$$MSE = \frac{1}{n} \sum_{i=1}^n (y_i - E(y_i|\theta))^2, \quad (7)$$

368 where y_i is the outcome of observation i and $E(y_i|\theta)$ gives the expected outcome given the pa-
369 rameters in the model θ . The MSE is easy to interpret, but is not always appropriate for models
370 fit with non-normal error structures (Gelman et al., 2014). A more general statistic for assessing
371 model predictions is the log pointwise predictive density (lppd) (Gelman et al., 2014). The lppd
372 for a given model is defined as,

$$lppd = \sum_{i=1}^n \log \int p(y_i|\theta) p_{post}(\theta) d\theta, \quad (8)$$

373 where the integral on the right side gives the probability of observing the outcome y at each data
374 point i given the full posterior distribution of the parameters in the model $p_{post}(\theta)$. In practice we
375 computed the lppd from the posterior simulations generated by STAN as,

$$\widehat{lppd} = \sum_{i=1}^n \log \left(\frac{1}{S} \sum_{s=1}^S p(y_i|\theta^S) \right), \quad (9)$$

376 where the summation of $p(y_i|\theta^S)$ gives the total probability of observing the the actual response y_i
377 given the simulated posterior distribution θ^S across the full set of model simulations S . The log of
378 this sum is then averaged across the set of all observations i . Higher lppd scores indicate that the
379 model better predicts the observations.

380 In addition, we evaluated whether the climate model predicted treatment effects of similar
381 direction and magnitude to those observed in the experiment. We did this by extracting the soil
382 moisture coefficients contained in ξ for each of the vital rates and then multiplying those by the
383 appropriate soil moisture covariates for each year and treatment level in the experiment. We then
384 averaged these across all five years in the experiment to find the average treatment effect predicted
385 by the climate model. We compared these to the posteriors of the treatment parameters, chi , from
386 the treatment model. As a measure of agreement between our predictions and observed response
387 we calculated the correlation between the predicted and observed treatment effects.

388 We considered the effect of climate covariates or treatment effects to be significant when
389 the 95% Bayesian credible intervals on the posterior estimates did not overlap zero.

390 All data and R code necessary to reproduce our analysis will be deposited in the Dryad
391 Digital Repository once the manuscript is accepted. The current version of the computer code
392 is available at <https://github.com/pbadler/ExperimentTests/tree/master/precip> and the data are
393 available at <https://bitbucket.org/ellner/driversdata>.

394 Results

395 Effects on soil moisture

396 Our treatments successfully changed the soil moisture in the experimental plots in the directions
397 expected (fig. 1). Spring spot measurements of soil moisture from all the plots showed that on
398 average the drought plots were roughly 50% drier, while irrigated plots were roughly 40% wetter
399 than ambient conditions (table 1).

400 The continuously recorded soil moisture data also showed treatment effects, but these were
401 weaker on average than the spot measurements and depended on season and recent rainfall (table
402 2; fig 2). We saw weaker effects during the spring than during the fall and summer: the drought
403 plots were about 20-30% drier than ambient in the fall and summer but only 7 to 14% drier during
404 the spring, while the irrigated plots were 30% wetter during the fall and summer but only 20-25%
405 wetter during the spring. Treatment differences were slightly larger during rainy periods, especially
406 in the spring (rainfall effect in table 2). We did not find evidence that the drought shelters and the
407 irrigation treatments consistently affected air temperature at 30 cm above the plots.

408 The SOILWAT soil moisture model predicted average monthly soil volumetric water content
409 of between 10 ml/ml and 15 ml/ml each month, with the month of April being the wettest and the
410 month of July, August and September being the driest on average. Annual variation in seasonal
411 soil moisture for each year was positively correlated with seasonal precipitation and negatively
412 correlated with seasonal temperature. During the course of the experiment, SOILWAT reproduced
413 much of the daily variation observed in soil moisture recorded by our automatic data loggers, but
414 the average soil moisture predicted by SOILWAT was about 5 ml/ml higher than the soil moisture
415 content observed in the field.

416 After adjusting the SOILWAT seasonal soil moisture predictions by the treatment effects,
417 we found that the soil moisture predicted in the drought plots during the course of the experiment
418 was well below the historical seasonal averages: the summer of 2012 and 2013, the fall of 2013, and
419 the spring and winter of 2014 fell below the 5th percentile limit for drought in the historical period
420 (fig 3). Soil moisture in our irrigation plots was generally above the historical average soil moisture
421 but conditions never exceeded the 90th percentile for soil moisture in the historical period (fig 3).

422 Effects on cover and vital rates

423 The cover of *H. comata* and *P. spicata* fell significantly in the drought plots from 2011 to 2016
424 (tables ??, ??; fig 4). The cover of *P. secunda* showed a slight decrease in the drought plots and
425 an increase in the irrigated plots but these changes were not significant (table ??). In contrast to
426 the grasses, the cover of *A. tripartita* increased slightly in all three treatments (fig 4).

427 Our treatment models fit to the experimental and observational data indicated a variety of
428 treatment effects on the vital rates of each species. Based on the WAIC scores with and without the
429 size by treatment effects, we retained size by treatment effects in the growth models for *A. tripartita*
430 and *P. secunda*, and the survival model for *P. secunda*. For *A. tripartita* we found significant size
431 by treatment effects of drought: drought had positive effects on plants of average size and smaller
432 (fig 5), but plants larger than the mean size by more than 1.5 standard deviations grew slightly less
433 in the drought treatment than in the controls. *A. tripartita* showed the opposite response in the
434 irrigated plots, (although the irrigation parameters were not significant at the 95% confidence level):
435 irrigation reduced growth for small plants while irrigation increased growth of plants more than
436 1.5 standard deviations larger than the mean size. Drought led to a strong (but not significant)

437 decrease in *H. comata* growth, while irrigation had no effect on growth. Like *A. tripartita*, we
438 saw size by treatment effects on *P. secunda* growth, with the negative effects of drought becoming
439 greater for larger plants. *P. secunda* showed the opposite response in the irrigation plots with larger
440 plants showing the largest increase in growth in response to irrigation (although not significant).
441 *P. spicata* growth was relatively unaffected by the drought and irrigation treatments.

442 Survival of all three grass species (fig 6) decreased in the drought plots. And *P. secunda*
443 showed a negative size by drought interaction effect: the survival of larger plants was more neg-
444 atively affected by drought than that of the smaller plants. *A. tripartita* survival was relatively
445 unaffected by the drought and irrigation treatments.

446 Recruitment in our irrigation plots was significantly less than in control plots for two grass
447 species *P. secunda* and *P. spicata* (fig 7). However, recruitment was also lower in the drought plots
448 than in the the control plots (although not significantly so), indicating that the decrease in the
449 irrigated plots may have not been entirely due to the irrigation itself. The recruitment data for *A.*
450 *tripartita* were relatively limited, with only 32 new recruits in total observed in all 30 plots over
451 the course of the five year experiment and we observed no treatment effects.

452 Consistent with previous research most of our demographic models estimated strong nega-
453 tive intra-specific crowding effects and weaker negative inter-specific crowding effects on the focal
454 species (appendix) (Adler et al., 2010; Chu et al., 2016; Chu and Adler, 2015; Adler et al., 2016).

455 Effects of soil moisture on vital rates

456 We choose three seasonal soil moisture variables for each species' based on their correlation with the
457 random year effects in the no climate model (table 4). We included size by soil moisture variables
458 for *A. tripartita* and *P. secunda* based on the treatment response we observed in the experiment.
459 All three time lags and all three seasons show up in the selected variables. After fitting the vital rate
460 models with the selected soil moisture variable we observed a trend towards positive soil moisture
461 effects on growth of all three grasses (fig 8). For *H.comata* the soil moisture of the most recent
462 summer (*summer*₁) had a significantly positive effect while the soil moisture during *summer*₀ and
463 *fall*_{lag} were also positive but not significant. For *A. tripartita* *fall*₀ and *summer*₀ had strong
464 negative effects on growth. There were also strong positive size by climate interaction effects for

465 these variables: soil moisture had a stronger negative effect on small plants and a positive effect
466 only on the largest plants (fig A-1).

467 Soil moisture had significant effects on the survival of all four species (fig 9). As for growth
468 the grasses showed mainly positive effects while *A. tripartita* showed a significant negative effect
469 of *summer₀* and a strong negative effect of *spring₀*. *H. comata* showed a significant positive effect
470 of *springlag* soil moisture and a strong positive effect of *spring₀* and *fall₁*. *P. secunda* showed a
471 significant positive effect of the previous *spring₀* and there was an interaction between this effect
472 and plant size: as plant size increased this effect became more positive. Finally for *P. spicata* there
473 was a significant positive effect of *springlag* soil moisture on survival.

474 There were only two significant effects of soil moisture on recruitment: *falllag* soil moisture
475 had a positive effect on *P. secunda*, and *summerlag* soil moisture had a negative effect on *P.*
476 *spicata* recruitment (fig 10). Soil moisture of *summer₀* also had a strong negative effect on *P.*
477 *spicata* recruitment.

478 The intra- and interspecific crowding effects estimated in the climate model were similar to
479 those estimated in the treatment model (appendix).

480 Evaluating the predictions

481 For most models adding climate covariates did not improve our ability to predict species responses
482 in the experiment (table 5). However, the climate models did improve overall prediction MSE for
483 growth of *A. tripartita* and growth and survival of *P. secunda* (table 5). In terms of lppd, the
484 climate model outperformed the no climate model in six out of twelve models: for *A. tripartita*
485 growth, *H. comata* recruitment, *P. secunda* growth and survival and *P. spicata* recruitment (table
486 5).

487 When we look at the predictions for each treatment separately we see that climate covariates
488 improved model predictions more often in the drought treatments than in the control or irrigation
489 treatments (table A-1). For all four species, the climate model outperformed the no climate model
490 for predicting the response of growth to drought in terms of lppd (table A-1). The climate model
491 also outperformed the no climate model for predicting irrigation effects on growth for all species
492 except *H. comata*.

493 Overall our climate models often predicted the correct direction of the drought and irriga-
494 tion treatments (fig 11). In four cases we both observed and predicted treatment effects significantly
495 different from zero based on the 95% Bayesian credible interval around the parameter mean: the
496 drought response of *H. comata* survival (fig A-6), the drought response of *P. secunda* growth (fig
497 A-3), the irrigation response of *P. spicata* recruitment (fig A-12) and the irrigation response of *P.*
498 *secunda* recruitment (fig A-11). In only one of these cases, for *P. secunda* recruitment, was the
499 predicted effect in the opposite direction from the observed treatment effect (fig 11). The overall
500 correlation between the predicted and observed treatment effects for all treatments, species and
501 vital rates was $r = 0.54$, whereas the correlation for the drought treatment effects, $r = 0.77$, was
502 better than for the irrigation effects, $r = 0.46$. Also the correlation between the size by climate and
503 size by treatment effects for *A. tripartita* growth and *P. secunda* growth and survival was much
504 stronger than the correlation between the intercept parameter estimates (fig 11).

505 Using the vital rate models for each species we generated one step ahead cover predictions
506 for each quadrat in each year of the experiment. Average cover predicted by the climate model
507 tended to be lower than the observed cover each year for *A. tripartita* and *P. secunda* (fig 12).
508 Comparing the overall population growth rates predicted to those observed in the experiment,
509 we see that the MSE of the climate model was lower than the MSE of the no climate model for
510 *P. secunda* and *P. spicata* (table 6). The predictions produced by the climate model for these
511 species were also slightly more correlated with the observations than the predictions produced by
512 the no climate model (table 6). Considering each treatment and species separately, the predicted
513 population growth rates for *A. tripartita*, *P. secunda* and *P. spicata* were all consistently lower
514 than the observed population growth rates (figs 13, 15, 16). The climate model showed lower MSE
515 for *A. tripartita*, *P. secunda* and *P. spicata* in the irrigation treatment, *P. spicata* in the control
516 treatment and *H. comata* in the drought treatment (fig 14). However, the correlations between the
517 predicted and observed log changes in cover did not always show the same pattern as MSE: the
518 climate model made more strongly correlated predictions with the observations than the no climate
519 model only for *P. spicata* and *P. secunda* in the control treatment and *P. secunda* and *H. comata*
520 in the drought treatment.

521 **Discussion**

522 Our experiment showed that observational data on the response of plant populations to interannual
523 climate variation can indeed help us predict the direction of species responses to experimental
524 climate manipulations (fig 11). The historical climate-demography correlations helped predict the
525 direction of experimental responses even though adding climate parameters to the demographic
526 models only improved vital rate predictions for half of the models (fig 5). This should give us some
527 hope that even when climate effects in demographic models fit to observational data are weak or
528 not significant, they may contain useful qualitative information on the direction of climate effects
529 in the future.

530 **Comparison of experimental and natural climate effects**

531 While previous studies in this system used the observational data to describe the effects of climate
532 on demography and survival, this is the first study to demonstrate effects of climate experimentally.
533 While previous studies of this system fit a variety of climate effects and used different modeling
534 approaches, we see many points of similarity between these studies in the responses of the four
535 dominant species to precipitation ((Chu et al., 2016),(Dalgleish et al., 2010), (Adler et al., 2012)).
536 First, in all three studies the strongest positive effects of precipitation among the four species are
537 reported for *H. comata*; this matches the negative effects of our drought experiment on this species
538 (fig 4). This effect is driven by a negative growth and survival response to drought (fig 5, 6).
539 On the other hand, if we had only conducted an irrigation experiment our results may not have
540 shown this consistency with previous work as *H. comata* showed no positive response to irrigation.
541 Previous studies also reported positive effects of precipitation on the other grasses, *P. secunda* and
542 *P. spicata*. Again our results are consistent with this result: drought led to declines in cover of
543 *P. spicata*, 4, and in the growth and survival of *P. secunda* (figs 5, 6). As for the *H. comata* the
544 magnitudes of drought effects were greater than the irrigation effects on these grasses.

545 The effects of precipitation on *A. tripartita* are more complicated. Previous research re-
546 ported negative direct effects of precipitation on this species ((Adler et al., 2012), (Chu et al.,
547 2016)). This effect has always seemed odd because it is hard to imagine why precipitation would
548 have a direct negative effect on a species in this dry ecosystem. But again the largely positive

549 (but size dependent) effects of drought treatments on *A. tripartita* growth should give us more
550 confidence in the negative effects of precipitation shown in the historical data. These studies also
551 report relative strong indirect effects of precipitation on *A. tripartita* mediated by its competition
552 with grasses. It is possible that some of the positive effect on *A. tripartita* growth in our drought
553 plots is the result of reduced grass cover (fig 12; (Chu et al., 2016)). However, our growth model
554 includes interspecific crowding and so should take into account any changes in grass abundance
555 that could be driving a positive response from *A. tripartita*. This leaves us with the question of
556 why this species would show a positive direct response to drought. Although there is some evidence
557 that saturated soils in the spring are detrimental for big sagebrush (*A. tridentata*), a closely related
558 species (Sturges, 1989; Germino and Reinhardt, 2014), soil saturation would conservatively seem to
559 require soils to be above 30 or 40% volumetric water content for several weeks, something that we
560 did not observe (fig 2). Another possible explanation is that our drought treatments reduced snow
561 cover in the winter and early spring, an effect that has been shown to benefit related sagebrush
562 species in other ecosystems (Perfors et al., 2003).

563 Overall we were somewhat surprised by the weak effects that reducing water availability
564 by 50% and increasing water availability by 150% had in this arid system. Cross-biome studies
565 of the relationship between precipitation and ANPP generally show that arid systems are highly
566 sensitive to water limitation (Huxman et al., 2004). We have two explanations for the seemingly
567 weak effects of precipitation we observed on demography. First, we measure the size of the pernnial
568 bunchgrasses in this system by their basal cover, which may not have a strong relationship with
569 their annual production. It is likely that we would find larger effects of precipitation on these
570 grasses if we had a more complete measurement of aboveground biomass. Moreover, much of the
571 growth of these species may be going into roots.

572 Another explanation for the weak effects of precipitation are that perennial species in this
573 cold desert ecosystems are well adapted to tolerate drought, either through escaping drought by
574 growing early in the year, or by avoiding drought stress later in the year through high water use
575 efficiency (Bazzaz, 1979; Franks, 2011). Indeed our soil moisture data generally show a pulse of
576 soil moisture in the spring when many grasses are actively growing (fig 2). Likewise, *A. tripartita*
577 is more deeply rooted than the grasses and able to continue its growth throughout the growing
578 season by drawing from deeper soil water (Germino and Reinhardt, 2014). The adaptations of

579 native perennial plants in cold deserts could make them less sensitive to water availability than
580 species in a more mesic ecosystem.

581 **Can the past predict the future?**

582 Our second research question was whether we could use long term observational data on species
583 response to precipitation to predict the response of each species to the experiment. Using the IBM,
584 we to generate predicted changes in population size for each year, we found that climate model
585 predictions were indeed better than the no climate models for two species: *P. spicata* and *P. secunda*
586 (table 6). In the drought treatment our one step ahead cover predictions for *H. comata* and *P.*
587 *secunda* were also better than the no climate model. Moreover, we also found that climate models
588 produced better predictions of species vital rates for half of the species/vital rate combinations we
589 tested (table 5). The rate of overall improvement in predictive ability produced by the climate
590 models over the no climate models was similar to the results reported by (Adler et al., 2013) who
591 also reported improved population-level predictions for half of the species predicted. Likewise, in
592 a within sample cross-validation analysis, (Tredennick et al., 2016) found that including climate
593 covariates improved population level predictions for two out of four species in a mixed grass prairie
594 in Montana.

595 We also compared the treatment parameters from the treatment model fit to the experimen-
596 tal data to the treatment parameters predicted by the climate model fit only to the observational
597 data 11. Among all the climate effects we predicted and observed, there were only four cases where
598 vital rate predictions and observations were both significantly different from zero (fig 11) and three
599 of these cases we successfully predicted the direction of the treatment effects. However, for *P. se-*
600 *cunda* recruitment we predicted a positive response of irrigation, but observed a negative response
601 (figs 11). From a statistical standpoint this is our arguably our greatest error in prediction. How-
602 ever, recruitment decreased in both the drought and irrigation plots for *P. secunda* and also for *P.*
603 *spicata* (fig 7). So its likely the decrease in *P. secunda* recruitment in the irrigated plots was due
604 to underlying differences in the set of experimental plots from the historical control plots rather
605 than the precipitation treatments.

606 The drought effects we observed on the three grasses were often stronger than the effects
607 we predicted, while the irrigation effects observed were often weaker than predicted (figs A-2, A-6,

608 A-3, A-7, A-4, A-8). In this water limited system, we expected that experimental irrigation would
609 lead to increases in plant performance, but we saw few cases where irrigation benefited any of the
610 plants. A pattern qualitatively similar to this shows up in both natural and experimental data
611 comparing precipitation to ANPP: decreases in grassland ANPP induced by drought are often of
612 greater magnitude than increases in ANPP induced by experimental irrigation or by above average
613 precipitation ((Hsu and Adler, 2014; Gherardi and Sala, 2015)). If we had fit our growth and
614 survival models with a non-linear function for soil moisture, perhaps informed by more mechanistic
615 understanding of water limitation on the physiology of these plants, we may have made more
616 accurate predictions of the drought and irrigation effects (Ehrln et al., 2016).

617 Conclusion

618 Our results give us more confidence that observational data can be used to detect and predict the
619 effects of annual soil moisture variation on sagebrush steppe plants. This should encourage more
620 researchers to try and use observational data to predict population response to climate in both
621 experimental and natural settings (Houlahan et al., 2016; Ehrln et al., 2016). Nevertheless, our
622 success at predicting the short-term response of two out of four species to a simple precipitation
623 manipulation is not likely to impress applied ecologists and policymakers who often need accurate
624 predictions for the effects of climate change in large complex systems. Clearly more work is needed
625 to learn how to accurately predict the ecological responses of species to climate change. Towards
626 that goal, perhaps the best way forward is to conduct more tests like this one.

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Table 1: Estimated parameters from a mixed effects model fit to the spring soil moisture data. Parameter with s.e. are shown. Intercept gives soil moisture in ambient controls.

	Model 1
(Intercept)	8.81*** (1.54)
TreatmentDrought	-3.97*** (0.45)
TreatmentIrrigation	3.26*** (0.45)
AIC	3191.87
BIC	3222.92
Log Likelihood	-1588.93
Num. obs.	624
Num. groups: plot	24
Num. groups: PrecipGroup	8
Num. groups: date	5
Var: plot (Intercept)	0.45
Var: PrecipGroup (Intercept)	0.23
Var: date (Intercept)	11.24
Var: Residual	8.90

*** $p < 0.001$, ** $p < 0.01$, * $p < 0.05$

Tables

Table 6: MSE of predicted log cover changes and correlations between log cover changes predicted and observed. Predictions for the cover changes in the experimental plots were generated either from the climate or no climate models. Instances where the climate model made better predictions than the no climate model are indicated with the ”***”. ARTR = *A. tripartita*, HECO = *H. comata*, POSE = *P. secunda*, PSSP = *P. spicata*.

	species	stat	baseline model	climate model	diff	improved
1	ARTR	cor	0.48	0.19	-0.29	
2	ARTR	MSE	0.30	0.30	0.00	
3	HECO	cor	0.29	0.22	-0.07	
4	HECO	MSE	0.49	0.57	0.07	
5	POSE	cor	0.45	0.53	0.07	***
6	POSE	MSE	0.42	0.41	-0.01	***
7	PSSP	cor	0.36	0.38	0.03	***
8	PSSP	MSE	0.39	0.39	-0.01	***

Table 2: Treatment effects on soil moisture. Intercept refers to drought effects in fall not rainy conditions. Model fit to the continuously logged soil moisture data as well as the spot measurements collected from all plots in the spring.

	Model 1
(Intercept)	-0.57*** (0.16)
TreatmentIrrigation	1.23*** (0.03)
rainfallrainy	-0.05 (0.03)
seasonspring	0.27*** (0.02)
seasonsummer	0.15*** (0.02)
seasonwinter	0.25*** (0.02)
TreatmentIrrigation:rainfallrainy	0.18*** (0.03)
TreatmentIrrigation:seasonspring	-0.23*** (0.03)
TreatmentIrrigation:seasonsummer	-0.26*** (0.03)
TreatmentIrrigation:seasonwinter	-0.33*** (0.03)
rainfallrainy:seasonspring	-0.23*** (0.04)
rainfallrainy:seasonsummer	-0.07 (0.04)
rainfallrainy:seasonwinter	-0.07 (0.07)
AIC	14581.58
BIC	14695.49
Log Likelihood	-7274.79
Num. obs.	9133
Num. groups: simple_date	1596
Num. groups: PrecipGroup	8
Var: simple_date (Intercept)	0.00
Var: PrecipGroup (Intercept)	0.19
Var: Residual	2.50

*** $p < 0.001$, ** $p < 0.01$, * $p < 0.05$

Table 3: Treatment effects on log cover change for each species from start of experiment in 2011 to last year of experiment in 2016. Intercept gives control effects. ARTR = *A. tripartita*, HECO = *H. comata*, POSE = *P. secunda*, PSSP = *P. spicata*.

	ARTR	Estimate	Std.Error	t-value	Pr(> t)
(Intercept)	-0.28	0.46		-0.61	0.55
TreatmentDrought	0.94	0.77		1.21	0.24
TreatmentIrrigation	0.89	0.77		1.15	0.27
	HECO	Estimate	Std.Error	t-value	Pr(> t)
(Intercept)	0.40	0.26		1.54	0.15
TreatmentDrought	-3.00	0.58		-5.18	0.001
TreatmentIrrigation	-0.12	0.5		-0.25	0.81
	POSE	Estimate	Std.Error	t-value	Pr(> t)
(Intercept)	-0.72	0.46		-1.57	0.13
TreatmentDrought	0.03	0.82		0.03	0.97
TreatmentIrrigation	1.15	0.78		1.47	0.16
	PSSP	Estimate	Std.Error	t-value	Pr(> t)
(Intercept)	0.02	0.21		0.09	0.93
TreatmentDrought	-0.89	0.38		-2.34	0.03
TreatmentIrrigation	0.15	0.38		0.38	0.70

Table 4: Selected climate variables for each vital rate model for each species. Correlations and p-values between the chosen variables and the intercept of the no climate model are shown. For ARTR growth and POSE growth and survival, the correlations between the year effects on size and the soil moisture variables are also given. "f" = fall, "su" = summer, "sp" = spring. ARTR = *A. tripartita*, HECO = *H. comata*, POSE = *P. secunda*, PSSP = *P. spicata*.

vital_rate	species	climate variable	Int. cor.	p val.	Size cor.	Size p. val.
growth	ARTR	su.0	-0.49	0.02	0.26	0.26
growth	ARTR	f.0	-0.28	0.23	0.40	0.08
growth	ARTR	sp.1	0.17	0.45	-0.33	0.14
growth	HECO	su.1	0.69	0.00		
growth	HECO	su.0	0.50	0.02		
growth	HECO	f.lag	0.37	0.10		
growth	POSE	f.lag	0.31	0.17	-0.11	0.64
growth	POSE	su.lag	0.29	0.20	-0.20	0.38
growth	POSE	sp.1	0.26	0.25	-0.20	0.38
growth	PSSP	f.lag	0.34	0.13		
growth	PSSP	su.lag	0.25	0.27		
growth	PSSP	f.0	-0.22	0.34		
recruitment	ARTR	su.lag	-0.32	0.16		
recruitment	ARTR	su.0	-0.26	0.25		
recruitment	ARTR	sp.1	0.22	0.34		
recruitment	HECO	su.lag	-0.31	0.18		
recruitment	HECO	su.0	-0.30	0.18		
recruitment	HECO	f.lag	0.19	0.40		
recruitment	POSE	sp.1	0.49	0.02		
recruitment	POSE	f.lag	0.34	0.13		
recruitment	POSE	f.1	0.32	0.16		
recruitment	PSSP	su.lag	-0.52	0.02		
recruitment	PSSP	su.0	-0.48	0.03		
recruitment	PSSP	sp.0	0.30	0.19		
survival	ARTR	su.0	-0.60	0.00		
survival	ARTR	sp.0	-0.41	0.06		
survival	ARTR	su.1	-0.40	0.07		
survival	HECO	sp.0	0.44	0.04		
survival	HECO	sp.lag	0.43	0.05		
survival	HECO	f.1	0.33	0.14		
survival	POSE	sp.0	0.44	0.04	0.22	0.34
survival	POSE	sp.1	0.27	0.23	-0.46	0.04
survival	POSE	f.lag	-0.00	0.99	0.30	0.19
survival	PSSP	sp.0	0.36	0.11		
survival	PSSP	sp.lag	0.34	0.13		
survival	PSSP	su.1	0.26	0.26		

Table 5: Comparison of model predictions from climate model and no climate model for each species and vital rate. Two prediction scores are reported, MSE and lppd. Lower MSE indicates improved predictions whereas higher lppd indicates improved predictions. Instances where the climate model outperformed the no climate model are marked with “***” in the last column. ARTR = *A. tripartita*, HECO = *H. comata*, POSE = *P. secunda*, PSSP = *P. spicata*.

species	vital_rate	score	climate model	baseline model	diff	improved
ARTR	growth	lppd	-186.08	-189.17	3.09	***
ARTR	growth	MSE	0.55	0.55	-0.00	***
ARTR	recruitment	lppd	-79.05	-77.81	-1.24	
ARTR	recruitment	MSE	169.86	9.47	160.39	
ARTR	survival	lppd	-37.55	-36.42	-1.13	
ARTR	survival	MSE	0.06	0.06	0.00	
HECO	growth	lppd	-475.54	-454.36	-21.18	
HECO	growth	MSE	1.26	1.18	0.09	
HECO	recruitment	lppd	-149.43	-151.60	2.17	***
HECO	recruitment	MSE	288.16	235.57	52.59	
HECO	survival	lppd	-158.99	-147.06	-11.93	
HECO	survival	MSE	0.12	0.11	0.01	
POSE	growth	lppd	-1823.71	-1831.56	7.85	***
POSE	growth	MSE	1.72	1.73	-0.01	***
POSE	recruitment	lppd	-260.05	-257.46	-2.59	
POSE	recruitment	MSE	45.40	37.32	8.08	
POSE	survival	lppd	-698.06	-718.60	20.54	***
POSE	survival	MSE	0.14	0.14	-0.00	***
PSSP	growth	lppd	-1232.93	-1237.92	4.99	***
PSSP	growth	MSE	1.51	1.51	0.00	
PSSP	recruitment	lppd	-271.34	-273.94	2.60	***
PSSP	recruitment	MSE	79.09	42.68	36.41	
PSSP	survival	lppd	-332.47	-307.26	-25.21	
PSSP	survival	MSE	0.11	0.10	0.01	

Figures

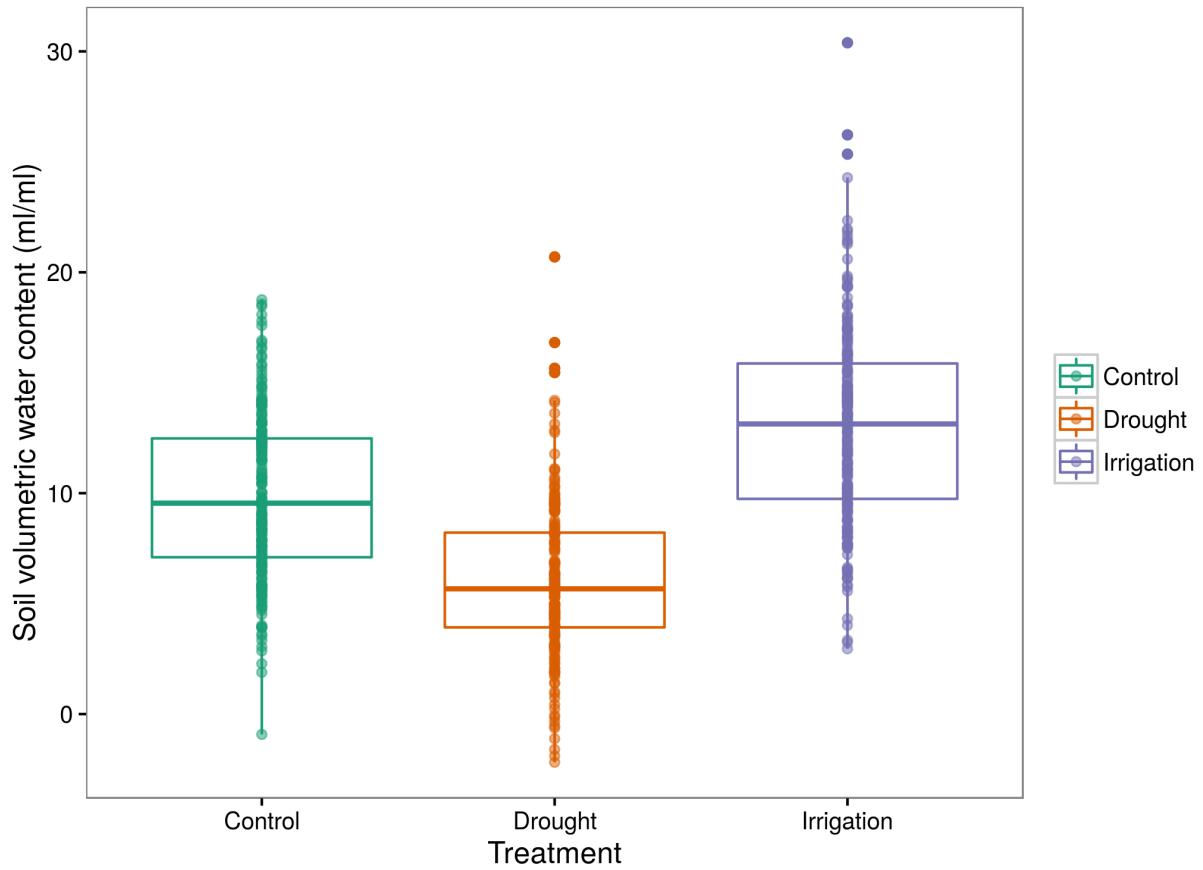


Figure 1: Soil moisture in the upper 5 cm of drought and irrigated plots compared to ambient controls. Soil moisture was measured at six locations around each plot at five different dates during the spring. Control plots were nearby areas of experiencing ambient soil moisture. Box plots show the median soil moisture and the interquartile range. Dots show individual soil moisture measurements. Readings of volumetric soil moisture less than zero were occasionally obtained in very dry soil.

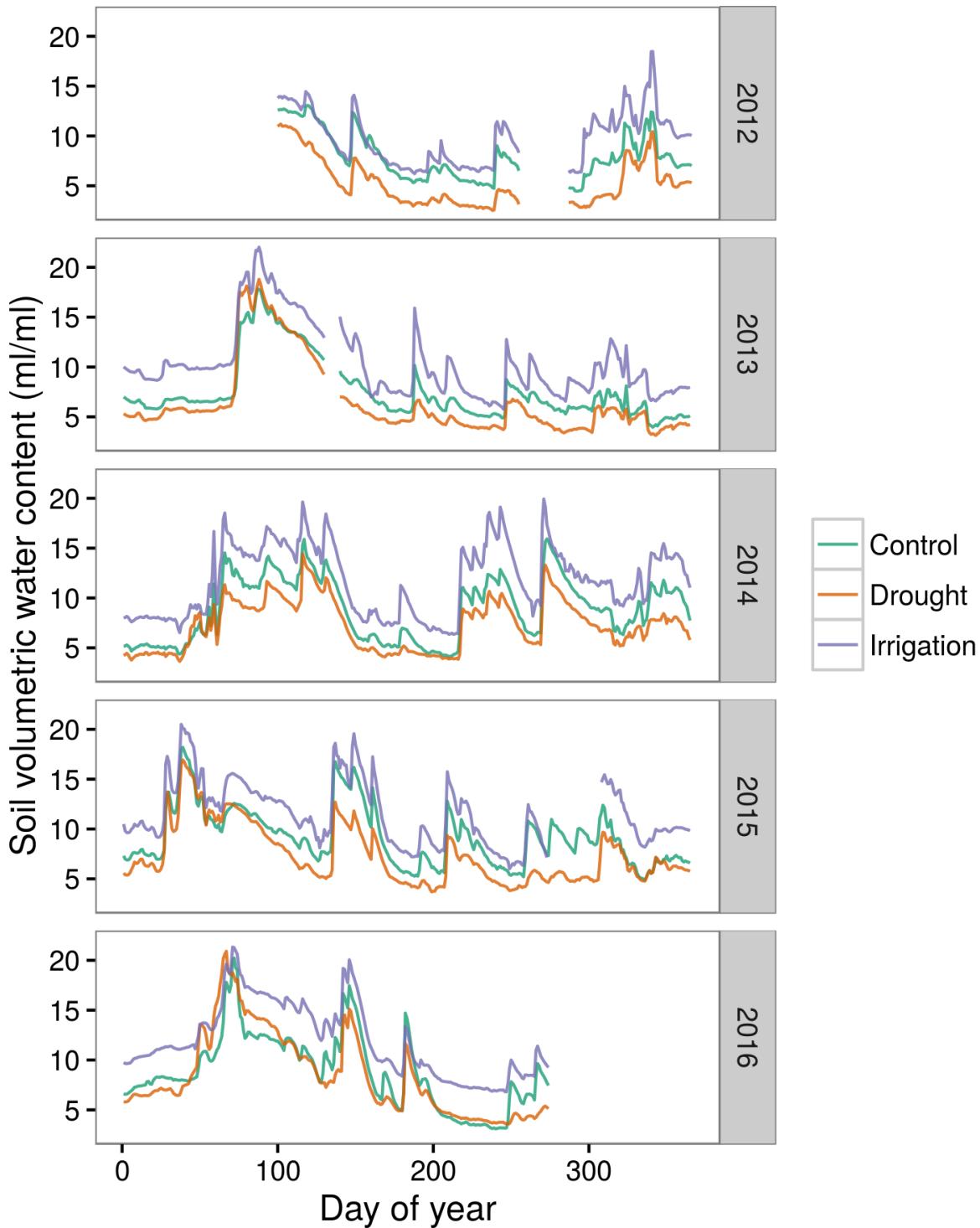


Figure 2: Average soil moisture in the control, drought, and irrigation treatments during each year of the experiment. Soil moisture was monitored in four drought plots, four irrigated plots and four ambient control plots. Two sensors were installed at 5 cm depth at each plot and two at 25 cm and data was logged every 2 hours.

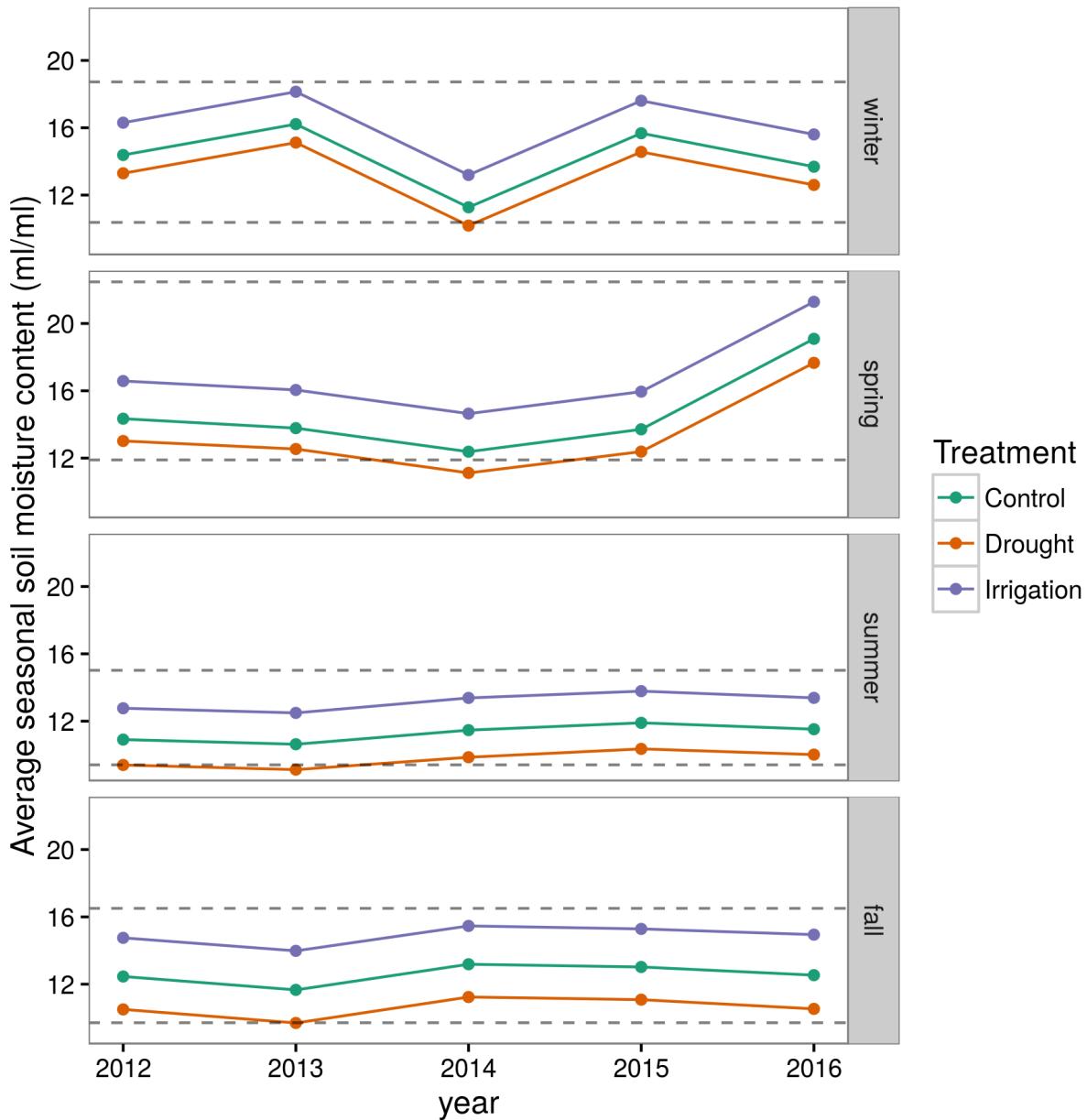


Figure 3: Average seasonal soil moisture in the control, drought, and irrigation treatments during each year of the experiment. The dashed gray lines give the 5th percentile and 95th percentile limits for seasonal soil moisture in the historical record (1929 to 2010).

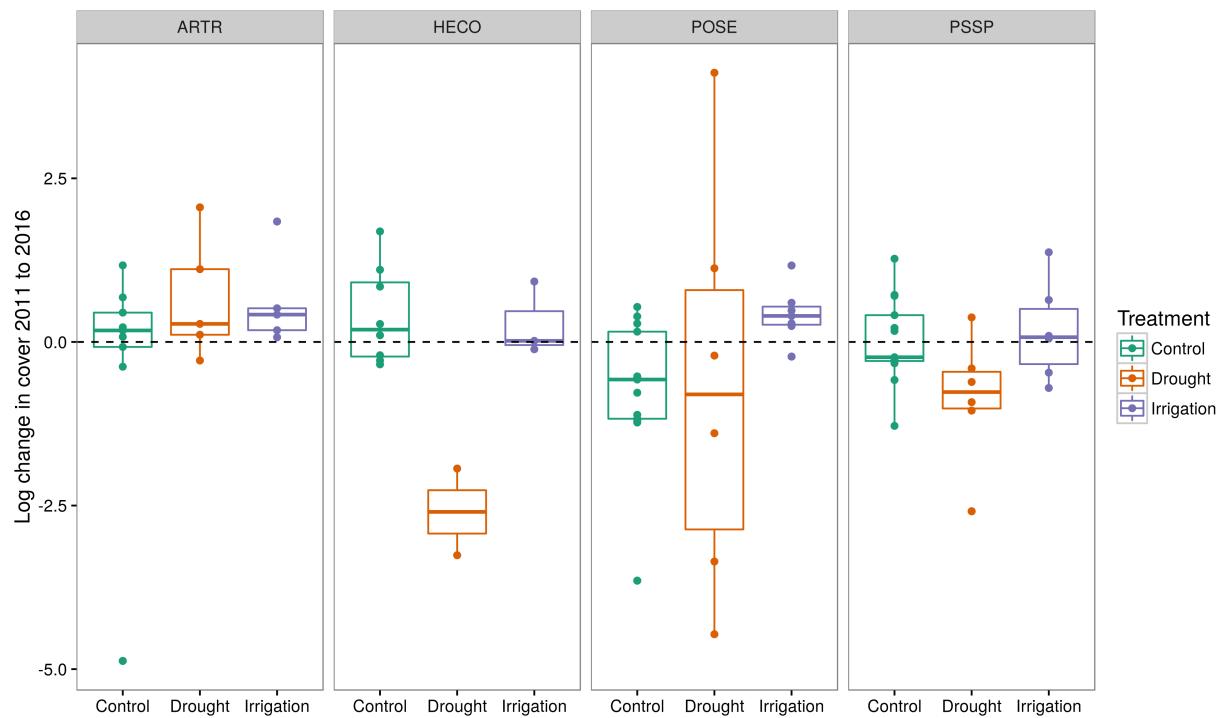


Figure 4: Log change in cover in each of the experimental plots from the pre-treatment monitoring in 2011 to the last year of the experiment in 2016. Box plots show the median cover change and the interquartile range. ARTR = *A. tripartita*, HECO = *H. comata*, POSE = *P. secunda*, PSSP = *P. spicata*.

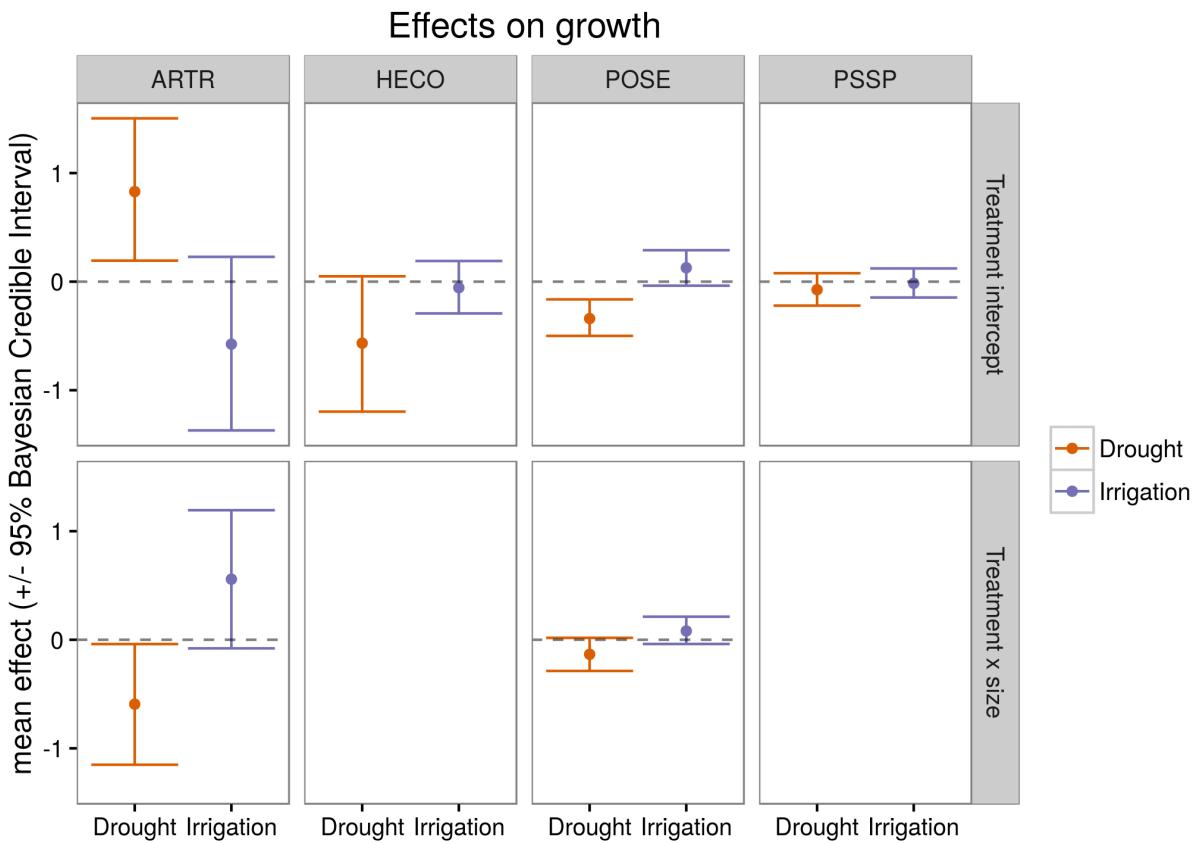


Figure 5: Parameter estimates for the effects of treatment on growth of all four species. We assessed a parameter as significant when the 95% Bayesian credible intervals did not overlap zero. Size by treatment interactions were only fit for ARTR, and POSE. Plant size was centered on mean size and scaled by its standard deviation. ARTR = *A. tripartita*, HECO = *H. comata*, POSE = *P. secunda*, PSSP = *P. spicata*.

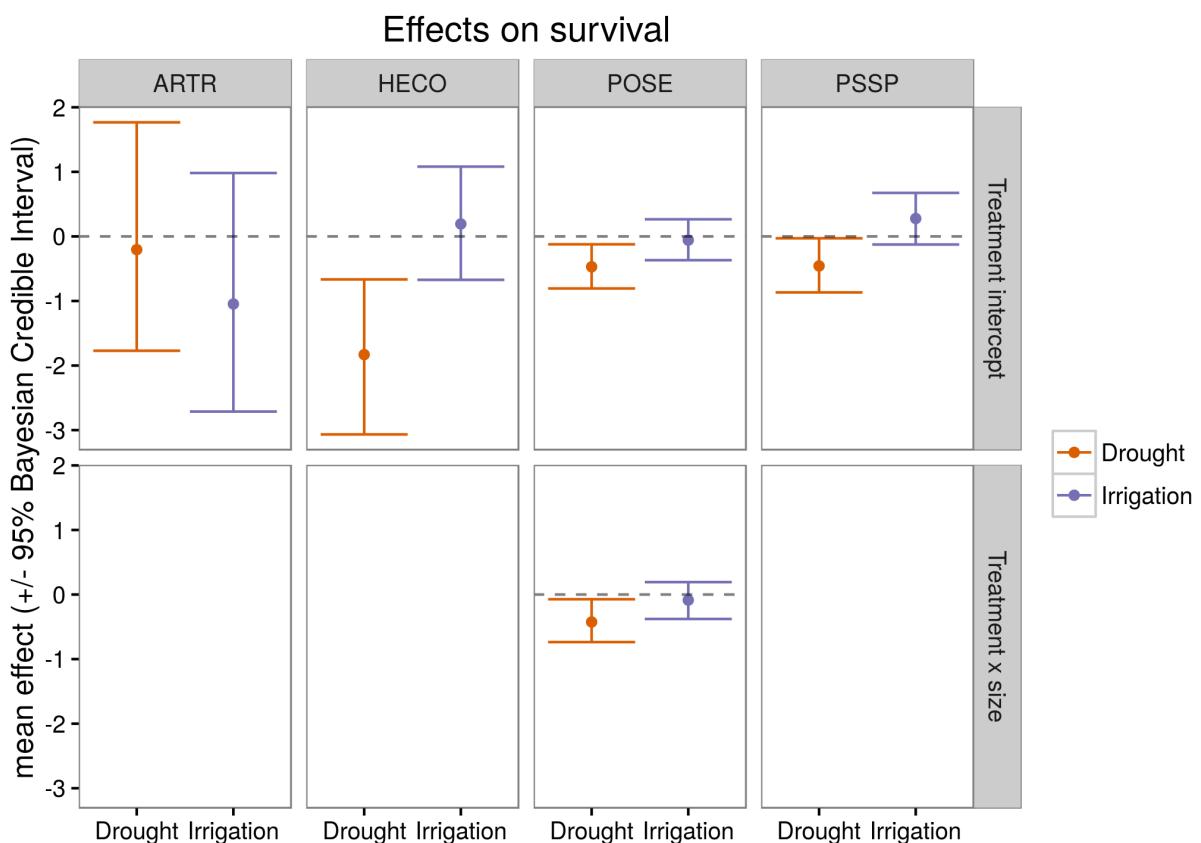


Figure 6: Parameter estimates for the effects of treatment on survival of all four species. We assessed a parameter as significant when the 95% Bayesian credible intervals did not overlap zero. Size by treatment interactions were only fit for POSE. Plant size was centered on mean size and scaled by its standard deviation. ARTR = *A. tripartita*, HECO = *H. comata*, POSE = *P. secunda*, PSSP = *P. spicata*.

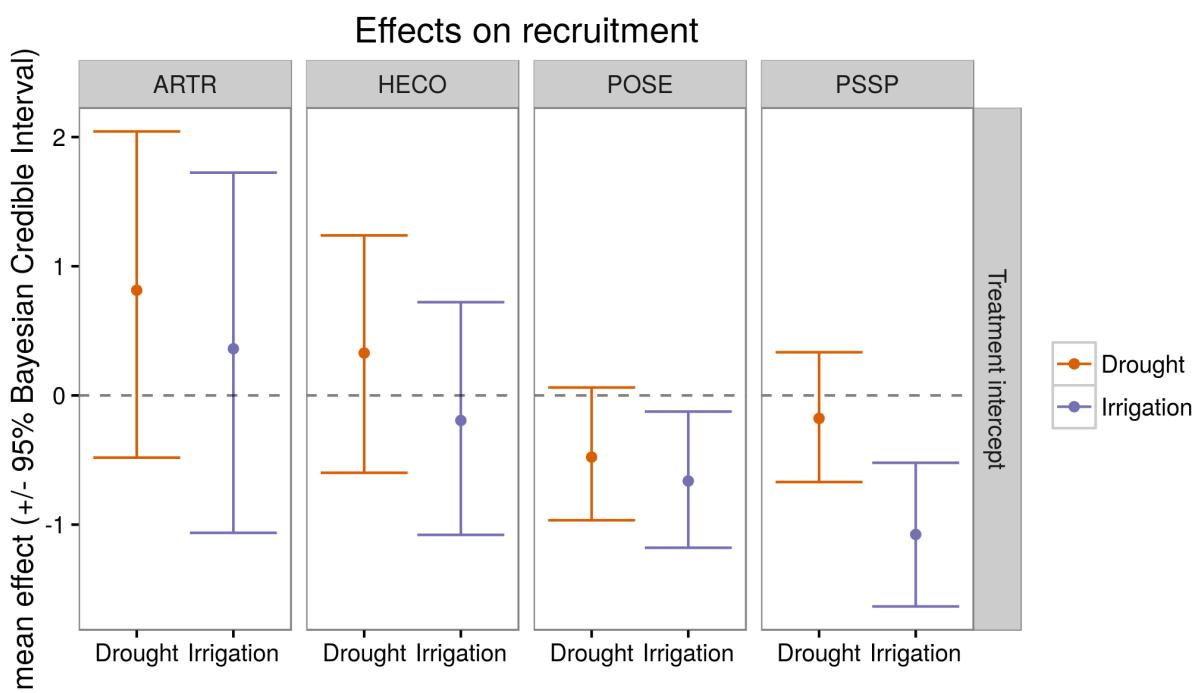


Figure 7: Parameter estimates for the effects of treatment on recruitment of all four species. We assessed a parameter as significant when the 95% Bayesian credible intervals did not overlap zero. ARTR = *A. tripartita*, HECO = *H. comata*, POSE = *P. secunda*, PSSP = *P. spicata*.

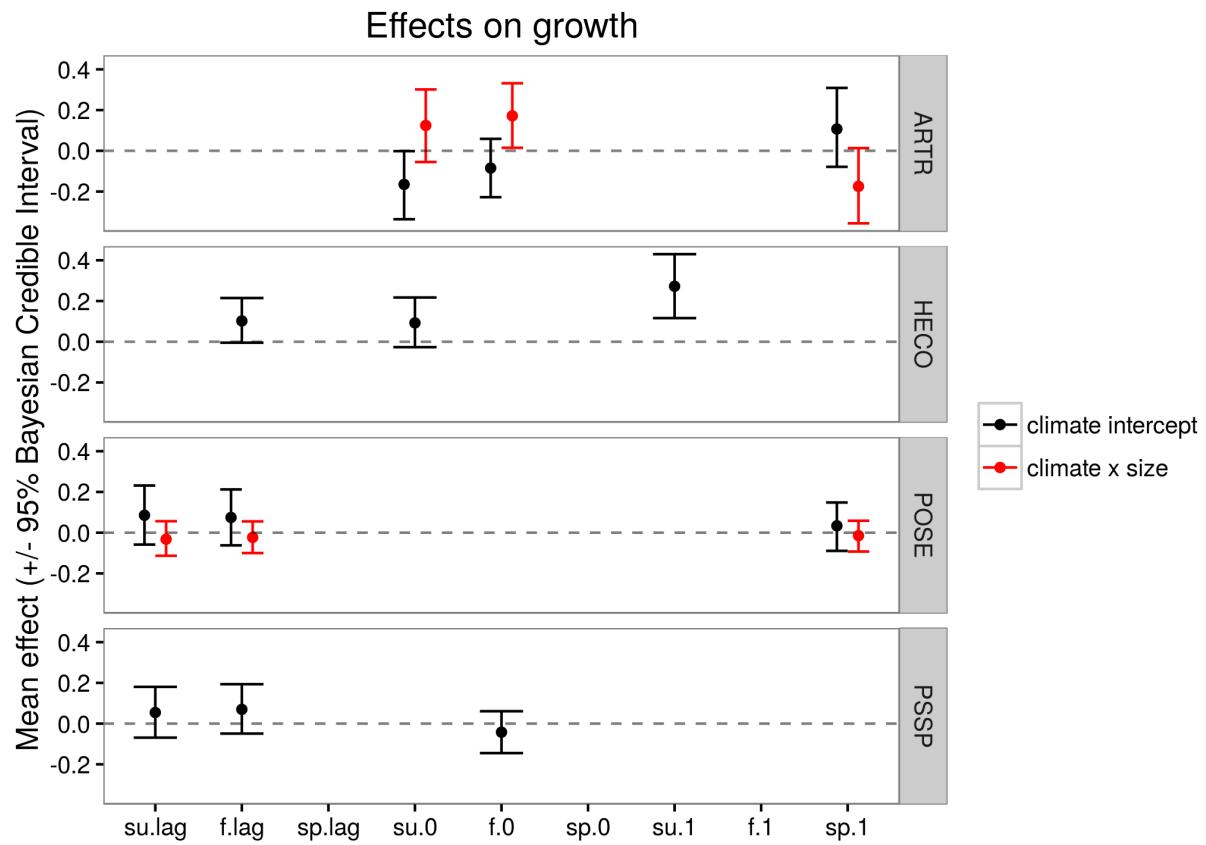


Figure 8: Parameter estimates for the selected seasonal soil moisture covariates on the growth of all four species. Parameters are ordered chronologically from most recent to the current growing season on the right to most distant on the left. Red parameters show size x climate interaction effects. We assessed a parameter as significant when the 95% Bayesian credible intervals did not overlap zero. ARTR = *A. tripartita*, HECO = *H. comata*, POSE = *P. secunda*, PSSP = *P. spicata*.

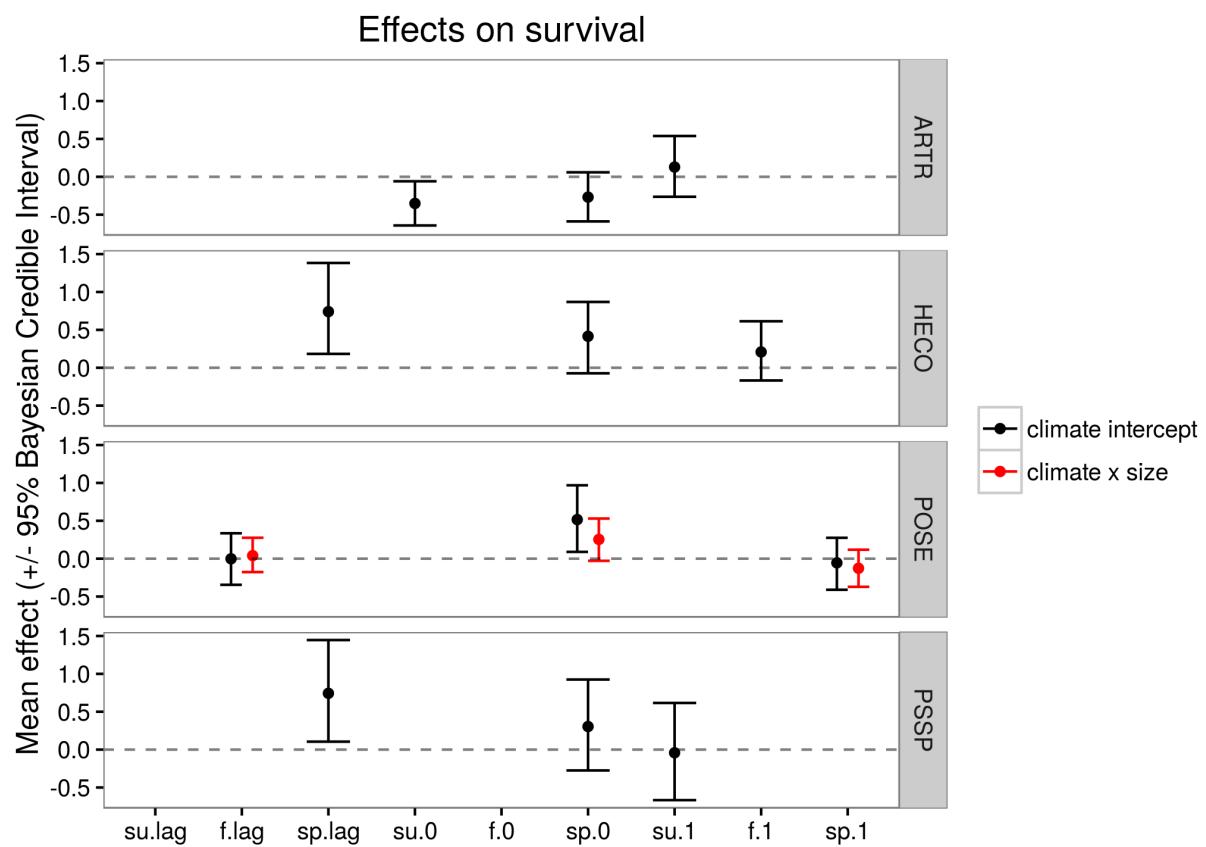


Figure 9: Parameter estimates for the selected seasonal soil moisture covariates on the survival of all four species. Parameters are ordered chronologically from most recent to the current growing season on the right to most distant on the left. Red parameters show size x climate interaction effects. We assessed a parameter as significant when the 95% Bayesian credible intervals did not overlap zero. ARTR = *A. tripartita*, HECO = *H. comata*, POSE = *P. secunda*, PSSP = *P. spicata*.

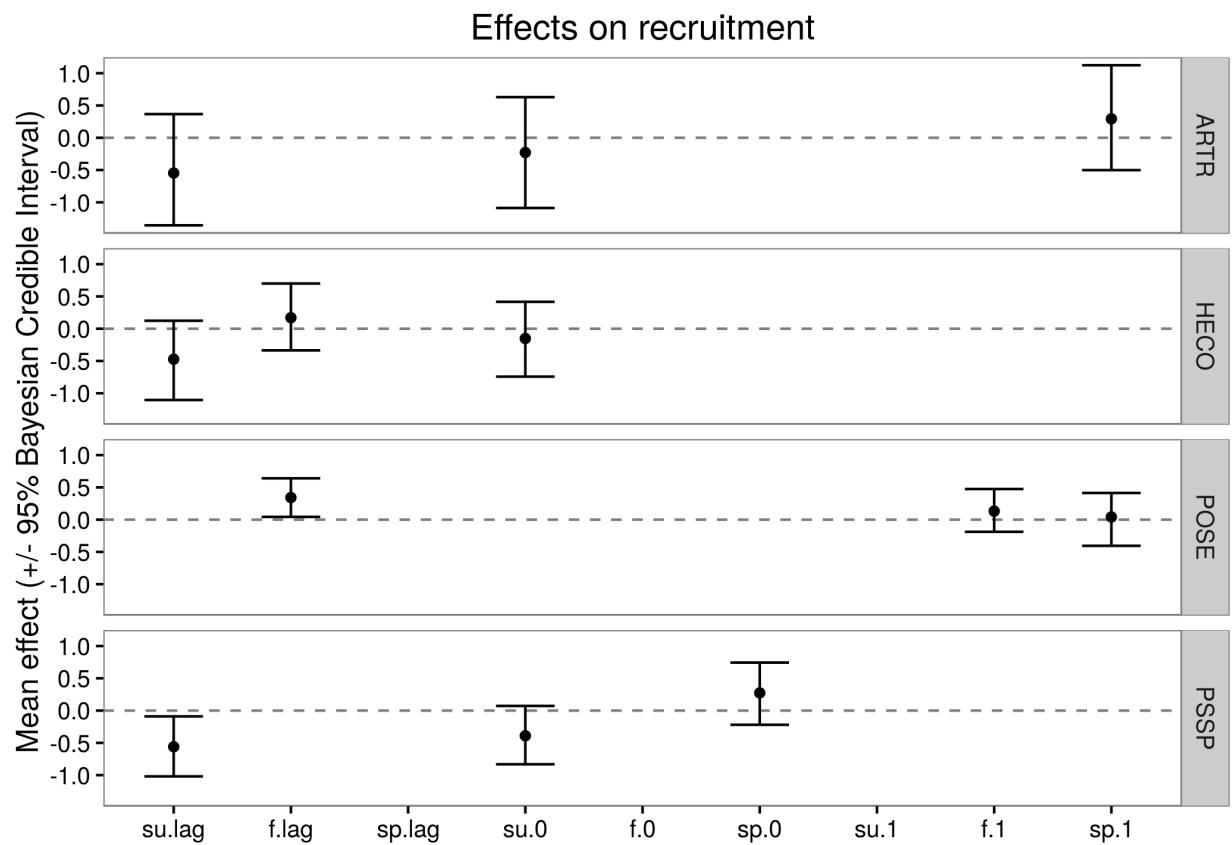


Figure 10: Parameter estimates for the selected seasonal soil moisture covariates on the recruitment of all four species. Parameters are ordered chronologically from most recent to the current growing season on the right to most distant on the left. We assessed a parameter as significant when the 95% Bayesian credible intervals did not overlap zero. ARTR = *A. tripartita*, HECO = *H. comata*, POSE = *P. secunda*, PSSP = *P. spicata*.

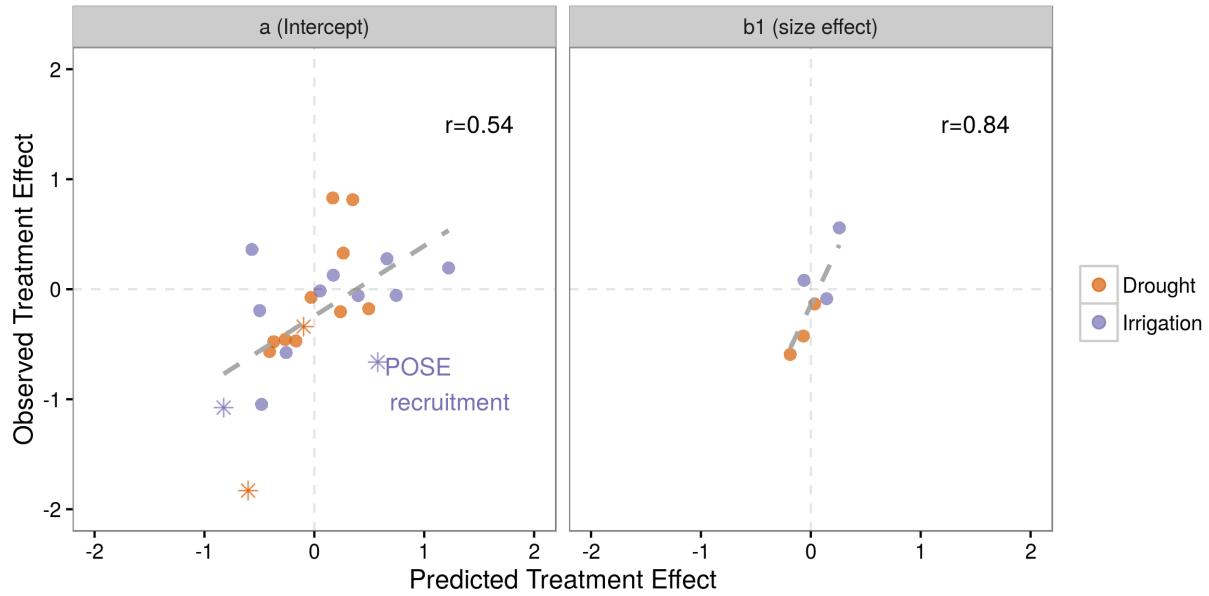


Figure 11: The treatment effects predicted by the climate model compared to the treatment effects observed for the intercept parameters (left side) and size by climate/treatment effects (right side). Parameters from all species and vital rates are shown together. The observed treatment effects come from the treatment model fitted to all the data including the five years of the experiment. The predicted parameters come from the climate model fitted to all years of observational data but do not include the five years of the experiment (2011 to 2016). Treatment parameters that were both observed and predicted to be significantly different from zero are shown with the “*” symbol. The correlation between predicted and observed parameters is given on each panel. *P. secunda* recruitment was predicted to be positively affected by the irrigation treatment but was in fact negatively affected. The other significant effects were in the correct direction. We assessed a parameter as significant when the 95% Bayesian credible intervals did not overlap zero.

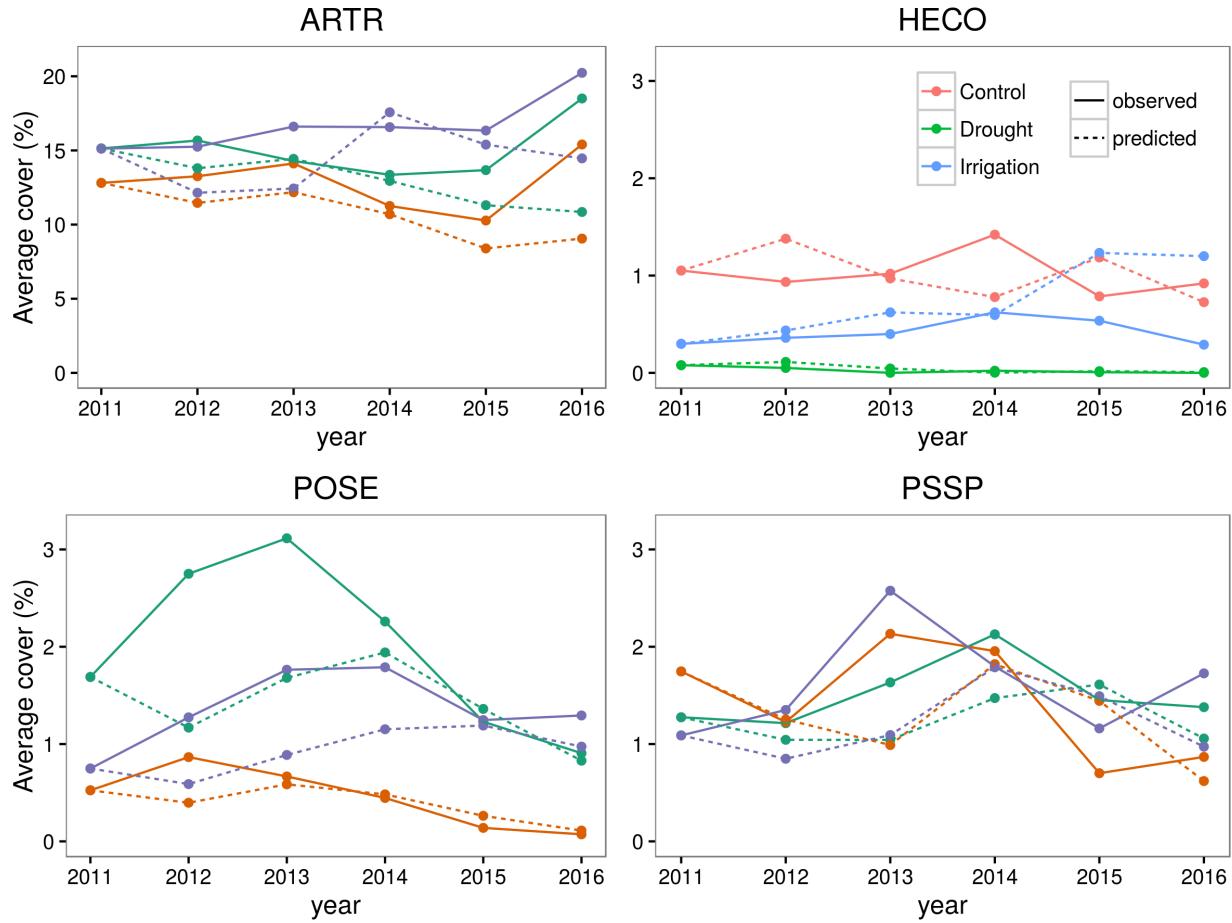


Figure 12: Observed average cover per quadrat in the experimental and control plots and one step ahead cover predictions from the climate model. Cover predictions for each year are generated from the IBM based on the observed distribution of plants in each quadrat in the current year. Quadrat cover was not predicted for the first year of the experiment in 2011. Note the different cover scales for ARTR and the three grass species. ARTR = *A. tripartita*, HECO = *H. comata*, POSE = *P. secunda*, PSSP = *P. spicata*.

A. tripartita

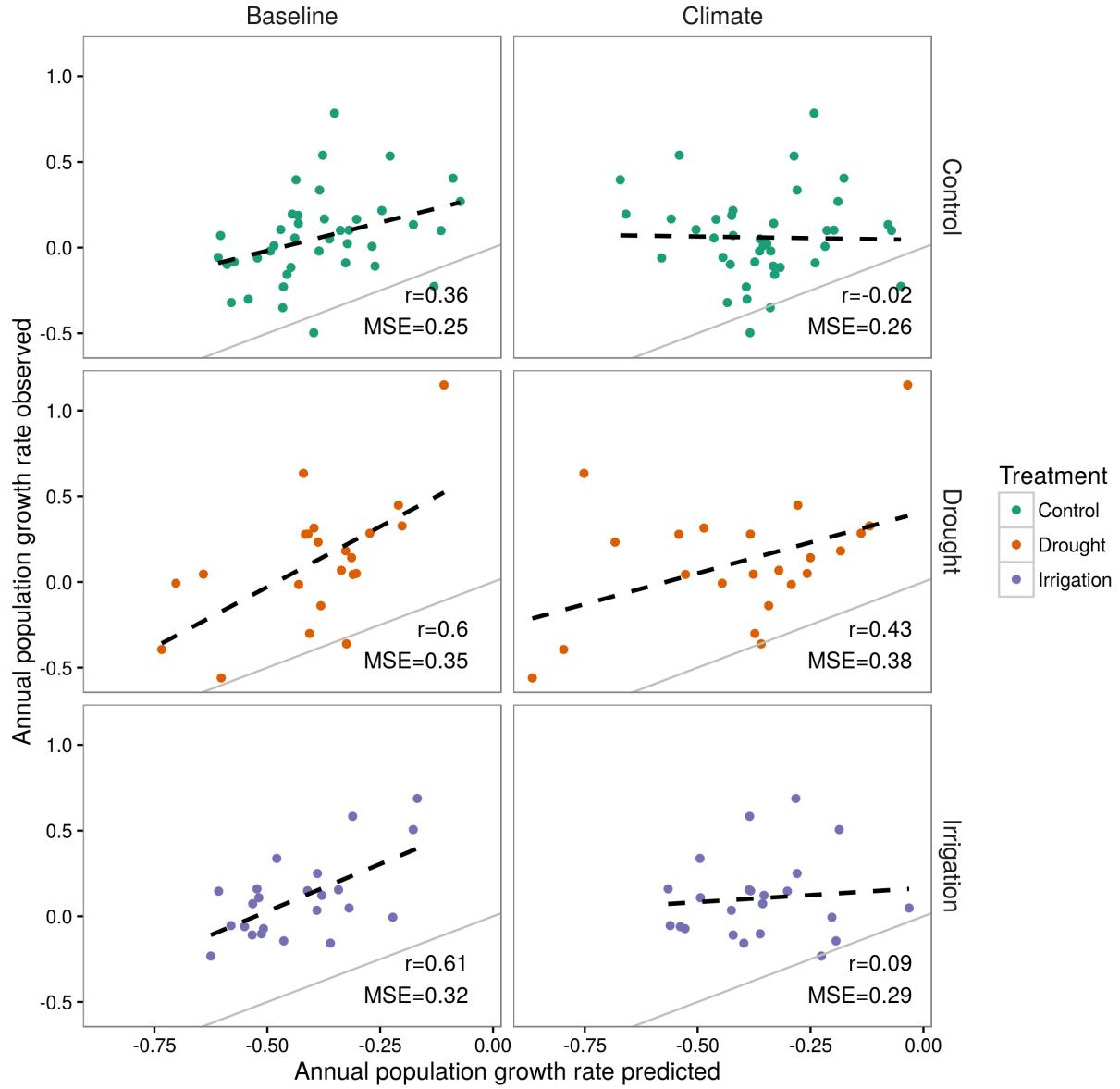


Figure 13: Observed and predicted one step ahead log change in *A. tripartita* cover in the experiment. Changes in cover predicted by the climate model are shown on the left and those predicted by the no climate model are shown on the right. Correlations coefficients between predictions and observations and MSE are shown for each treatment and model. Gray line shows 1:1 line.

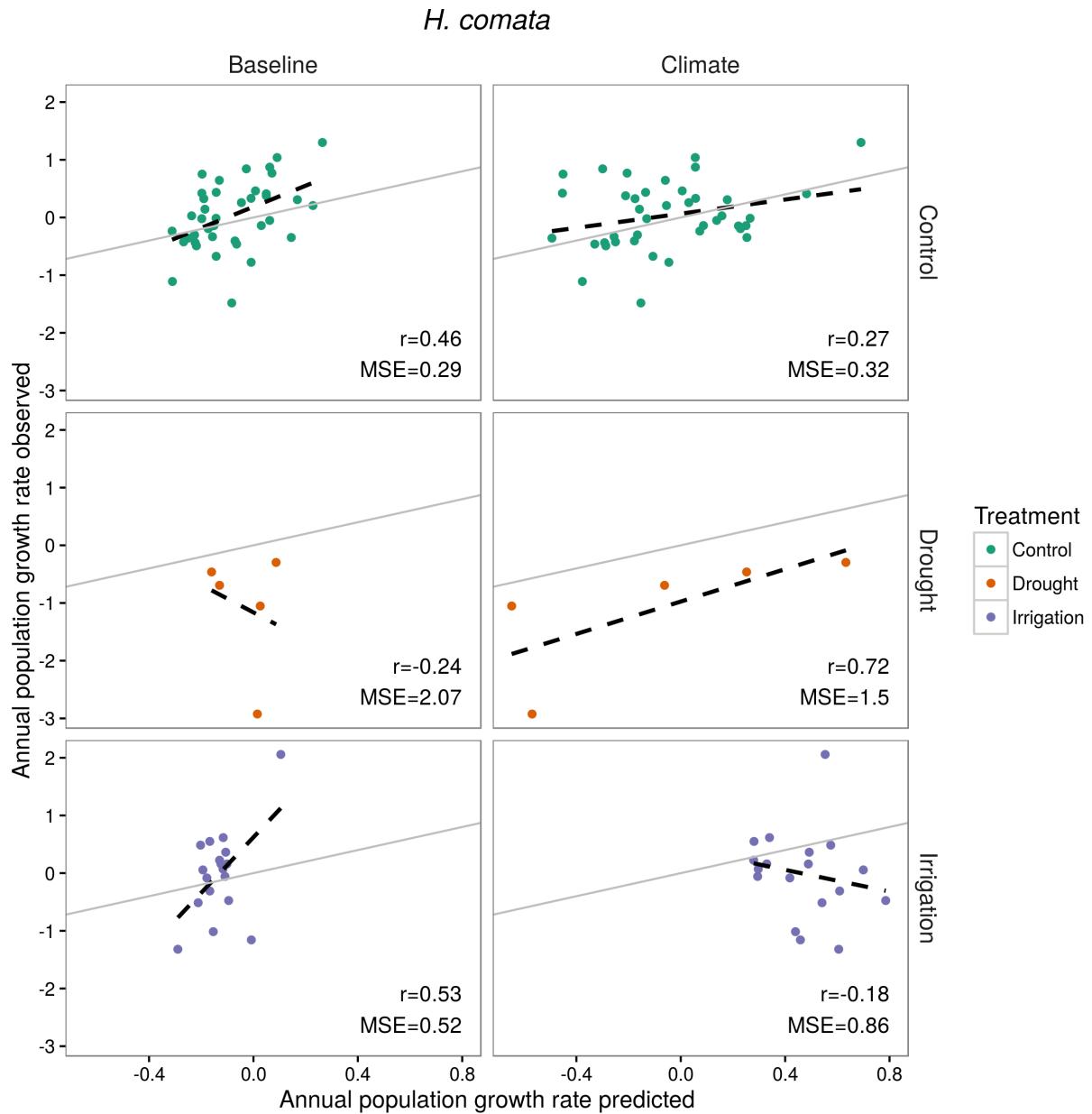


Figure 14: Observed and predicted one step ahead log change in *H. comata* cover in the experiment. Changes in cover predicted by the climate model are shown on the left and those predicted by the no climate model are shown on the right. Correlations coefficients between predictions and observations and MSE are shown for each treatment and model. Gray line shows 1:1 line.

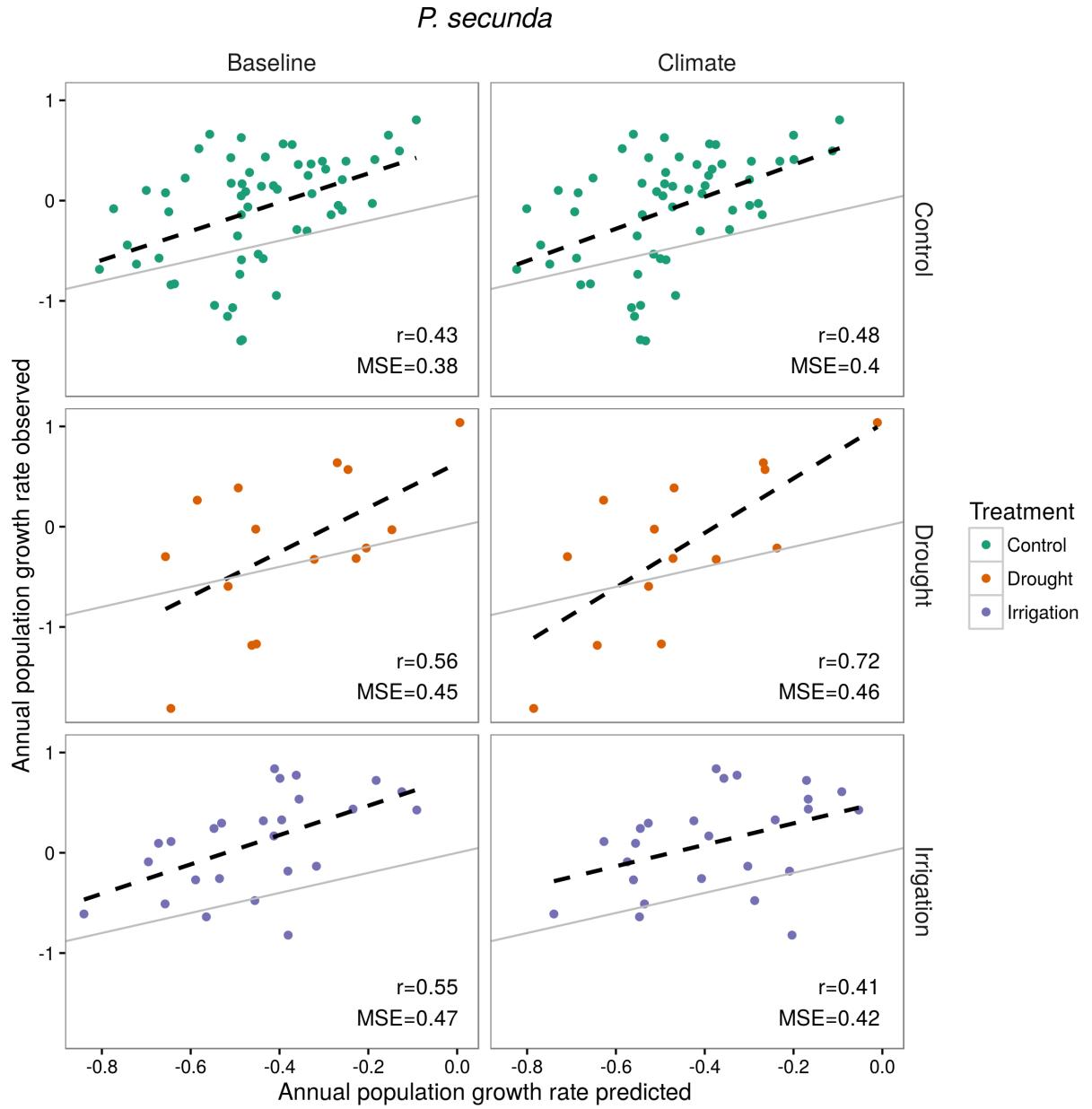


Figure 15: Observed and predicted one step ahead log change in *P. secunda* cover in the experiment. Changes in cover predicted by the climate model are shown on the left and those predicted by the no climate model are shown on the right. Correlations coefficients between predictions and observations and MSE are shown for each treatment and model. Gray line shows 1:1 line.

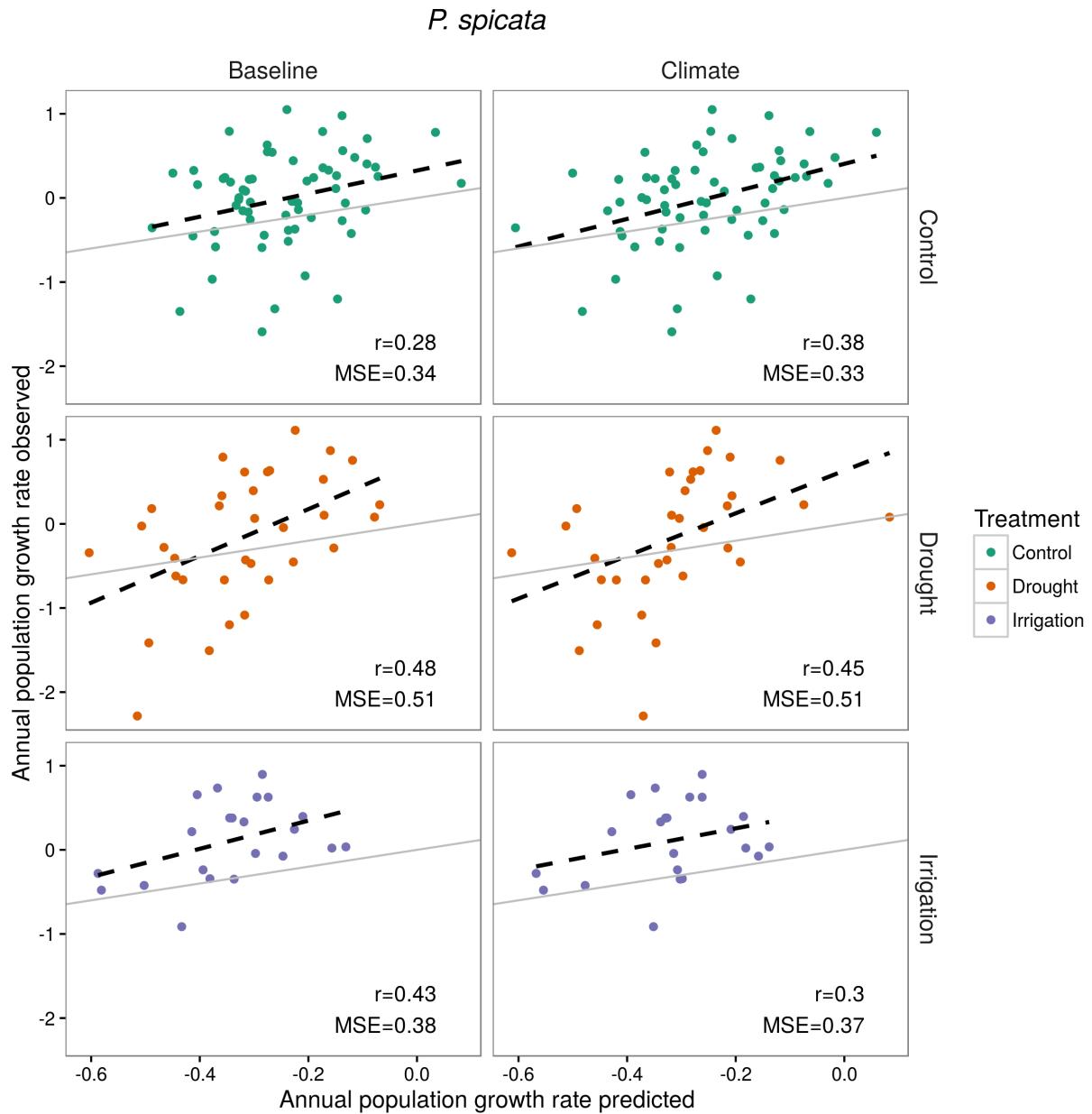


Figure 16: Observed and predicted one step ahead log change in *P. spicata* cover in the experiment. Changes in cover predicted by the climate model are shown on the left and those predicted by the no climate model are shown on the right. Correlations coefficients between predictions and observations and MSE are shown for each treatment and model. Gray line shows 1:1 line.

Appendix

Additional Tables

Table A-1: Comparison of model predictions from climate model and no climate model for each species and vital rate and treatment. Two prediction scores are reported, MSE and lppd. Lower MSE indicates improved predictions whereas higher lppd indicates improved predictions. Instances where the climate model outperformed the no climate model are marked with “***” in the last column. ARTR = *A. tripartita*, HECO = *H. comata*, POSE = *P. secunda*, PSSP = *P. spicata*.

	species	vital_rate	Treatment	score	climate model	baseline model	diff	improved
1	ARTR	growth	Control	lppd	-107.53	-108.40	0.87	***
2	ARTR	growth	Control	MSE	0.57	0.56	0.01	
3	ARTR	growth	Drought	lppd	-39.71	-40.01	0.30	***
4	ARTR	growth	Drought	MSE	0.53	0.49	0.03	
5	ARTR	growth	Irrigation	lppd	-38.85	-40.75	1.91	***
6	ARTR	growth	Irrigation	MSE	0.50	0.57	-0.07	***
7	ARTR	recruitment	Control	lppd	-32.61	-31.05	-1.56	
8	ARTR	recruitment	Control	MSE	61.88	10.59	51.29	
9	ARTR	recruitment	Drought	lppd	-28.93	-26.52	-2.41	
10	ARTR	recruitment	Drought	MSE	523.95	11.62	512.33	
11	ARTR	recruitment	Irrigation	lppd	-17.51	-20.24	2.73	***
12	ARTR	recruitment	Irrigation	MSE	4.72	5.34	-0.62	***
13	ARTR	survival	Control	lppd	-24.19	-23.06	-1.13	
14	ARTR	survival	Control	MSE	0.07	0.07	0.00	
15	ARTR	survival	Drought	lppd	-5.48	-5.34	-0.13	
16	ARTR	survival	Drought	MSE	0.04	0.04	-0.00	***
17	ARTR	survival	Irrigation	lppd	-7.88	-8.01	0.13	***
18	ARTR	survival	Irrigation	MSE	0.06	0.06	-0.00	***
19	HECO	growth	Control	lppd	-377.77	-369.46	-8.31	
20	HECO	growth	Control	MSE	1.11	1.09	0.02	
21	HECO	growth	Drought	lppd	-8.74	-10.97	2.23	***
22	HECO	growth	Drought	MSE	3.12	4.35	-1.23	***
23	HECO	growth	Irrigation	lppd	-89.03	-73.93	-15.10	
24	HECO	growth	Irrigation	MSE	2.02	1.47	0.55	
25	HECO	recruitment	Control	lppd	-93.35	-93.47	0.12	***

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	species	vital_rate	Treatment	score	climate model	baseline model	diff	improved
26	HECO	recruitment	Control	MSE	613.41	499.11	114.29	
27	HECO	recruitment	Drought	lppd	-25.39	-27.56	2.17	***
28	HECO	recruitment	Drought	MSE	1.94	2.33	-0.38	***
29	HECO	recruitment	Irrigation	lppd	-30.69	-30.56	-0.12	
30	HECO	recruitment	Irrigation	MSE	5.21	7.62	-2.41	***
31	HECO	survival	Control	lppd	-124.59	-112.70	-11.90	
32	HECO	survival	Control	MSE	0.12	0.11	0.01	
33	HECO	survival	Drought	lppd	-17.89	-20.82	2.93	***
34	HECO	survival	Drought	MSE	0.22	0.26	-0.05	***
35	HECO	survival	Irrigation	lppd	-16.51	-13.54	-2.97	
36	HECO	survival	Irrigation	MSE	0.09	0.07	0.02	
37	POSE	growth	Control	lppd	-1117.20	-1117.29	0.08	***
38	POSE	growth	Control	MSE	1.50	1.51	-0.00	***
39	POSE	growth	Drought	lppd	-254.17	-257.32	3.16	***
40	POSE	growth	Drought	MSE	2.66	2.69	-0.03	***
41	POSE	growth	Irrigation	lppd	-452.34	-456.95	4.61	***
42	POSE	growth	Irrigation	MSE	1.87	1.90	-0.03	***
43	POSE	recruitment	Control	lppd	-127.64	-128.73	1.09	***
44	POSE	recruitment	Control	MSE	35.20	44.82	-9.61	***
45	POSE	recruitment	Drought	lppd	-60.34	-63.15	2.80	***
46	POSE	recruitment	Drought	MSE	23.60	33.88	-10.28	***
47	POSE	recruitment	Irrigation	lppd	-72.06	-65.58	-6.48	
48	POSE	recruitment	Irrigation	MSE	85.04	27.63	57.41	
49	POSE	survival	Control	lppd	-366.49	-380.49	14.00	***
50	POSE	survival	Control	MSE	0.12	0.12	-0.00	***
51	POSE	survival	Drought	lppd	-175.29	-187.88	12.59	***
52	POSE	survival	Drought	MSE	0.21	0.22	-0.01	***
53	POSE	survival	Irrigation	lppd	-156.28	-150.23	-6.05	
54	POSE	survival	Irrigation	MSE	0.13	0.13	0.00	
55	PSSP	growth	Control	lppd	-627.07	-625.63	-1.44	
56	PSSP	growth	Control	MSE	1.38	1.36	0.02	
57	PSSP	growth	Drought	lppd	-292.90	-297.61	4.71	***
58	PSSP	growth	Drought	MSE	1.82	1.85	-0.03	***
59	PSSP	growth	Irrigation	lppd	-312.96	-314.67	1.71	***
60	PSSP	growth	Irrigation	MSE	1.51	1.51	-0.00	***
61	PSSP	recruitment	Control	lppd	-123.81	-125.23	1.42	***

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	species	vital_rate	Treatment	score	climate model	baseline model	diff	improved
62	PSSP	recruitment	Control	MSE	30.59	34.79	-4.20	***
63	PSSP	recruitment	Drought	lppd	-87.34	-86.58	-0.77	
64	PSSP	recruitment	Drought	MSE	222.16	54.58	167.58	
65	PSSP	recruitment	Irrigation	lppd	-60.18	-62.12	1.94	***
66	PSSP	recruitment	Irrigation	MSE	20.90	44.57	-23.67	***
67	PSSP	survival	Control	lppd	-148.69	-140.15	-8.54	
68	PSSP	survival	Control	MSE	0.10	0.09	0.01	
69	PSSP	survival	Drought	lppd	-83.26	-78.09	-5.17	
70	PSSP	survival	Drought	MSE	0.11	0.11	0.01	
71	PSSP	survival	Irrigation	lppd	-100.52	-89.02	-11.50	
72	PSSP	survival	Irrigation	MSE	0.13	0.11	0.01	

Additional Figures

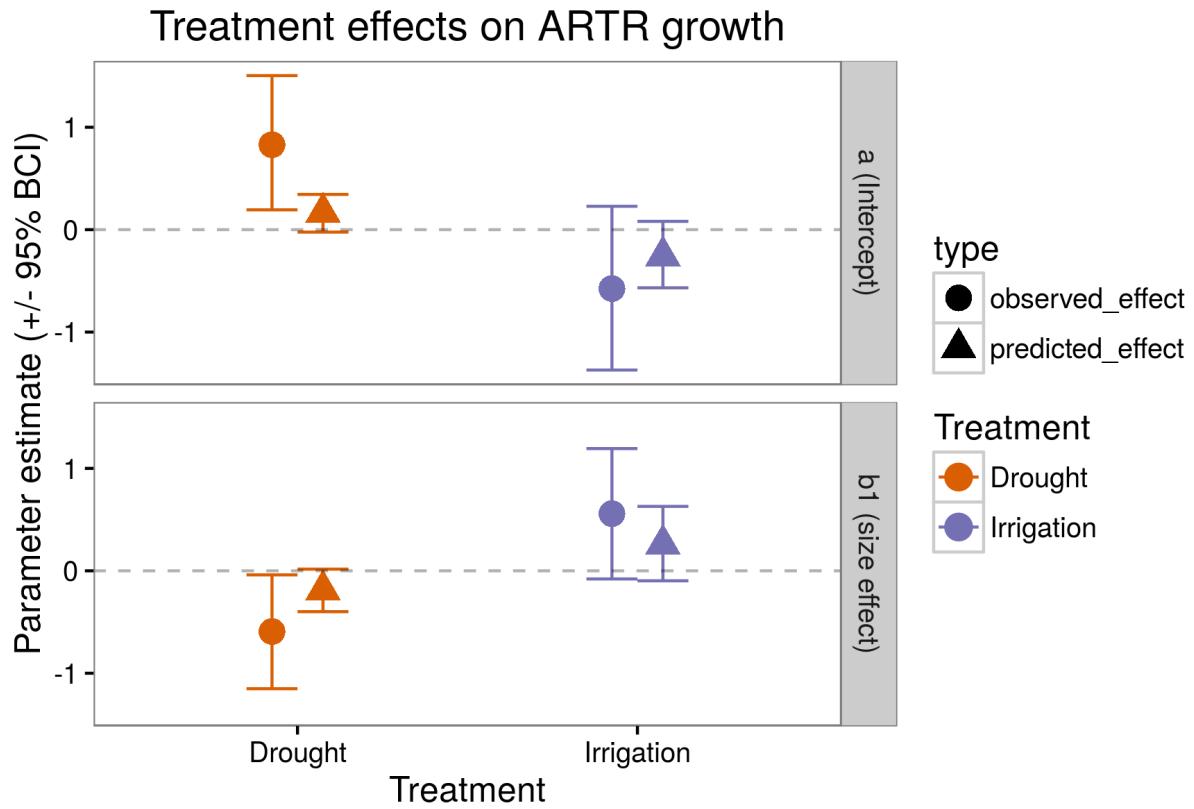


Figure A-1: Comparison of treatment effects predicted and observed for *A. tripartita* growth. Upper figure shows each parameter estimate separately while the lower figure shows the effect of treatment as a function of plant size. The observed treatment effects come from the treatment model fitted to all the data including the five years of the experiment. The predicted parameters come from the climate model fitted to all years of observational data but do not include the five years of the experiment (2011 to 2016). We assessed a parameter as significant when the 95% Bayesian credible intervals did not overlap zero.

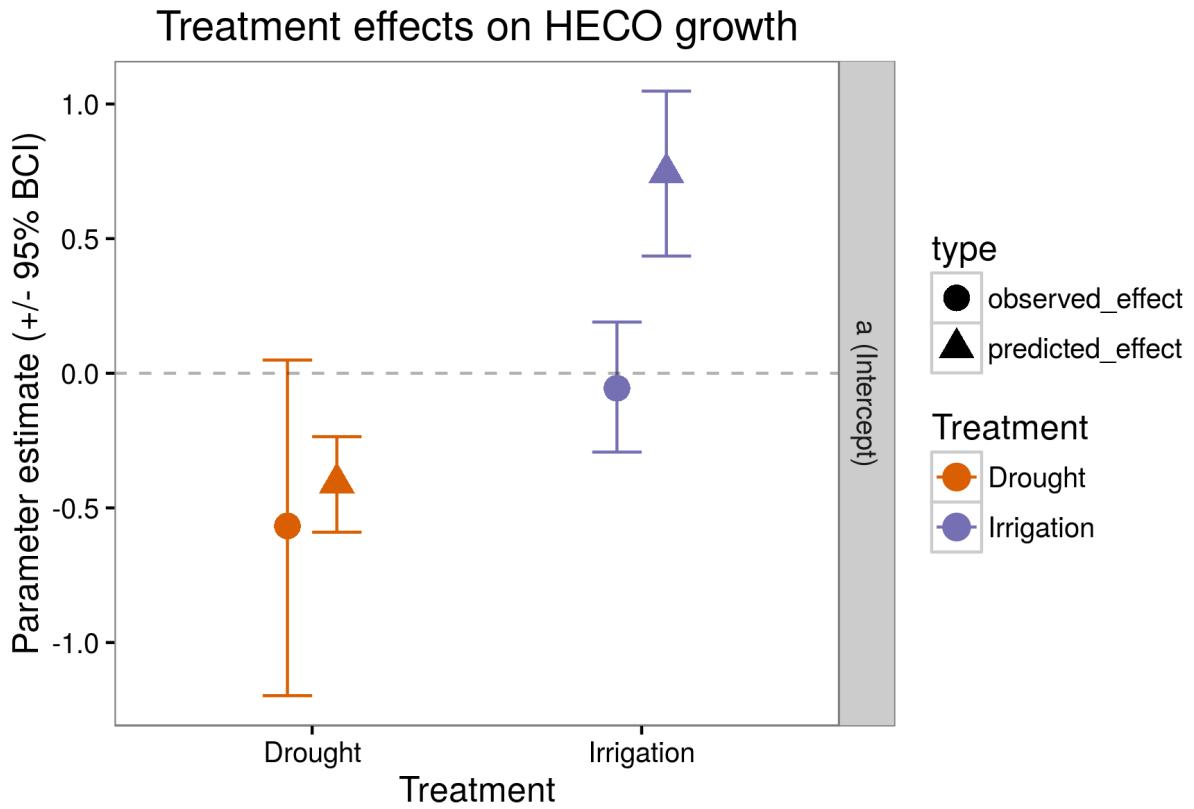


Figure A-2: Comparison of treatment effects predicted and observed for *H. comata* growth. The observed treatment effects come from the treatment model fitted to all the data including the five years of the experiment. The predicted parameters come from the climate model fitted to all years of observational data but do not include the five years of the experiment (2011 to 2016). We assessed a parameter as significant when the 95% Bayesian credible intervals did not overlap zero.

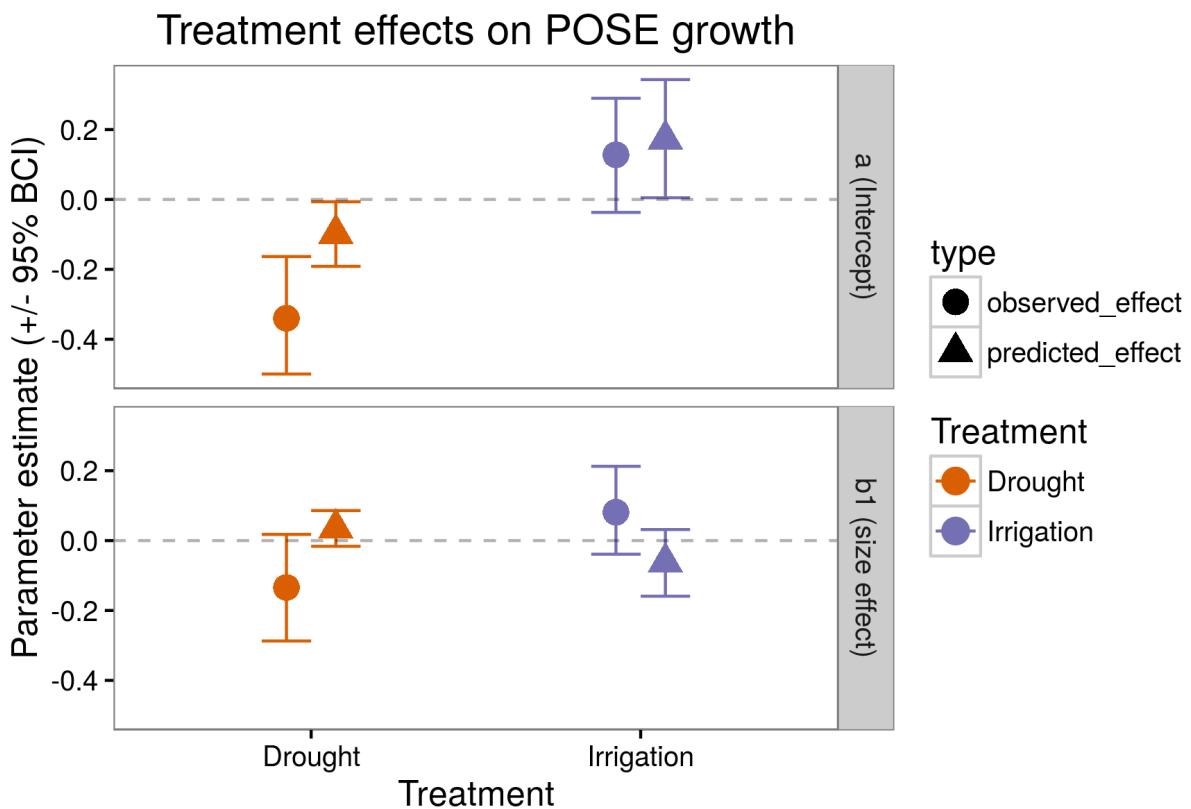


Figure A-3: Comparison of treatment effects predicted and observed for *P. secunda* growth. Upper figure shows each parameter estimate separately while the lower figure shows the effect of treatment as a function of plant size. The observed treatment effects come from the treatment model fitted to all the data including the five years of the experiment. The predicted parameters come from the climate model fitted to all years of observational data but do not include the five years of the experiment (2011 to 2016). We assessed a parameter as significant when the 95% Bayesian credible intervals did not overlap zero.

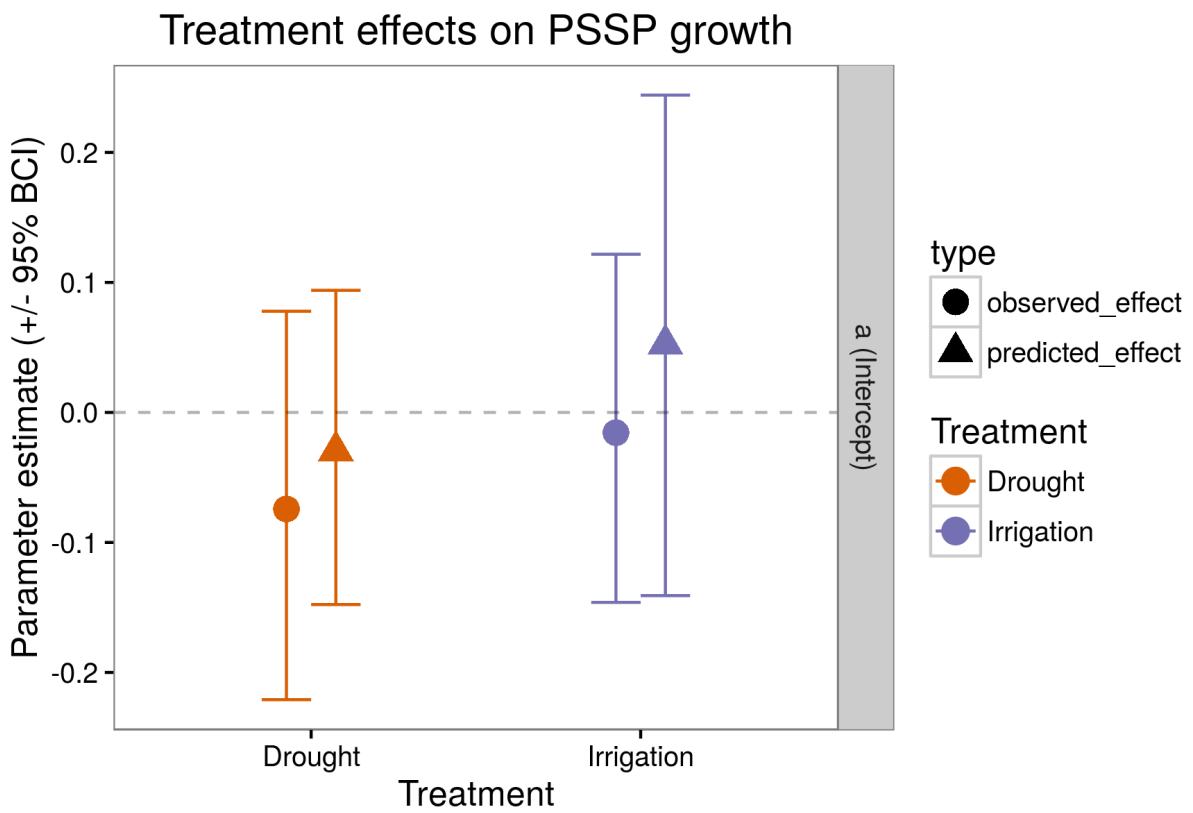


Figure A-4: Comparison of treatment effects predicted and observed for *P. spicata* growth. The observed treatment effects come from the treatment model fitted to all the data including the five years of the experiment. The predicted parameters come from the climate model fitted to all years of observational data but do not include the five years of the experiment (2011 to 2016). We assessed a parameter as significant when the 95% Bayesian credible intervals did not overlap zero.

Treatment effects on ARTR survival

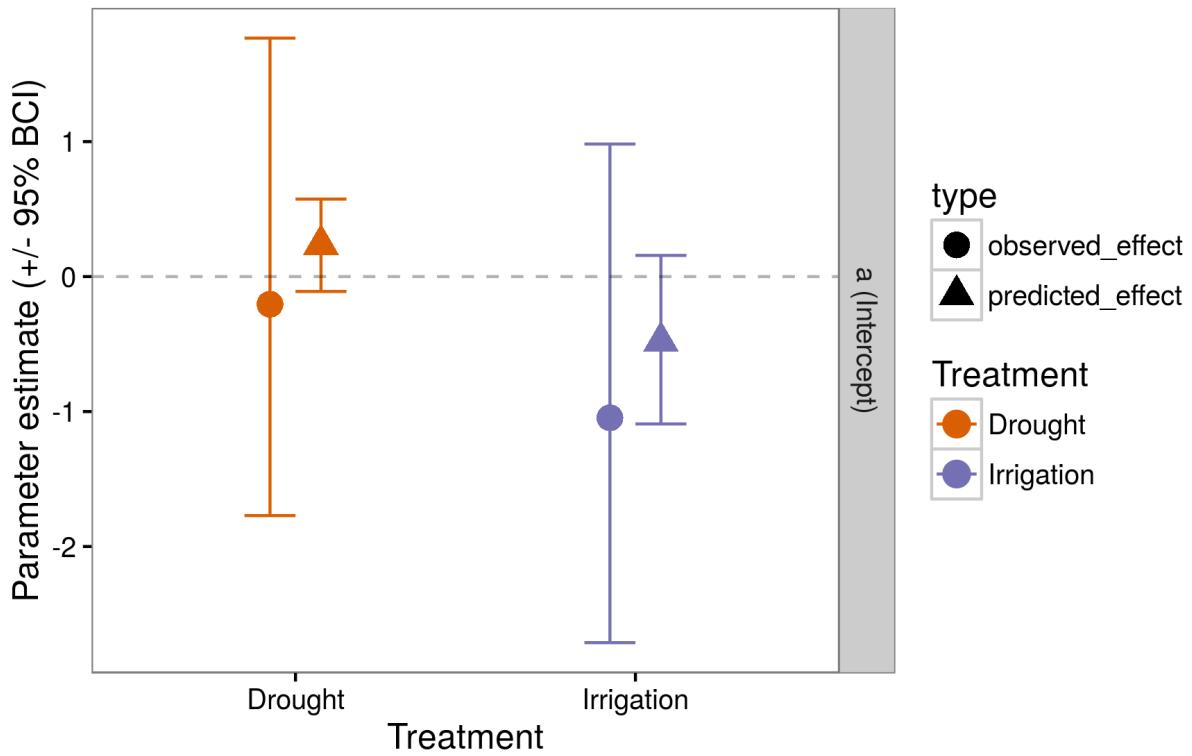


Figure A-5: Comparison of treatment effects predicted and observed for *A. tripartita* survival. The observed treatment effects come from the treatment model fitted to all the data including the five years of the experiment. The predicted parameters come from the climate model fitted to all years of observational data but do not include the five years of the experiment (2011 to 2016). We assessed a parameter as significant when the 95% Bayesian credible intervals did not overlap zero.

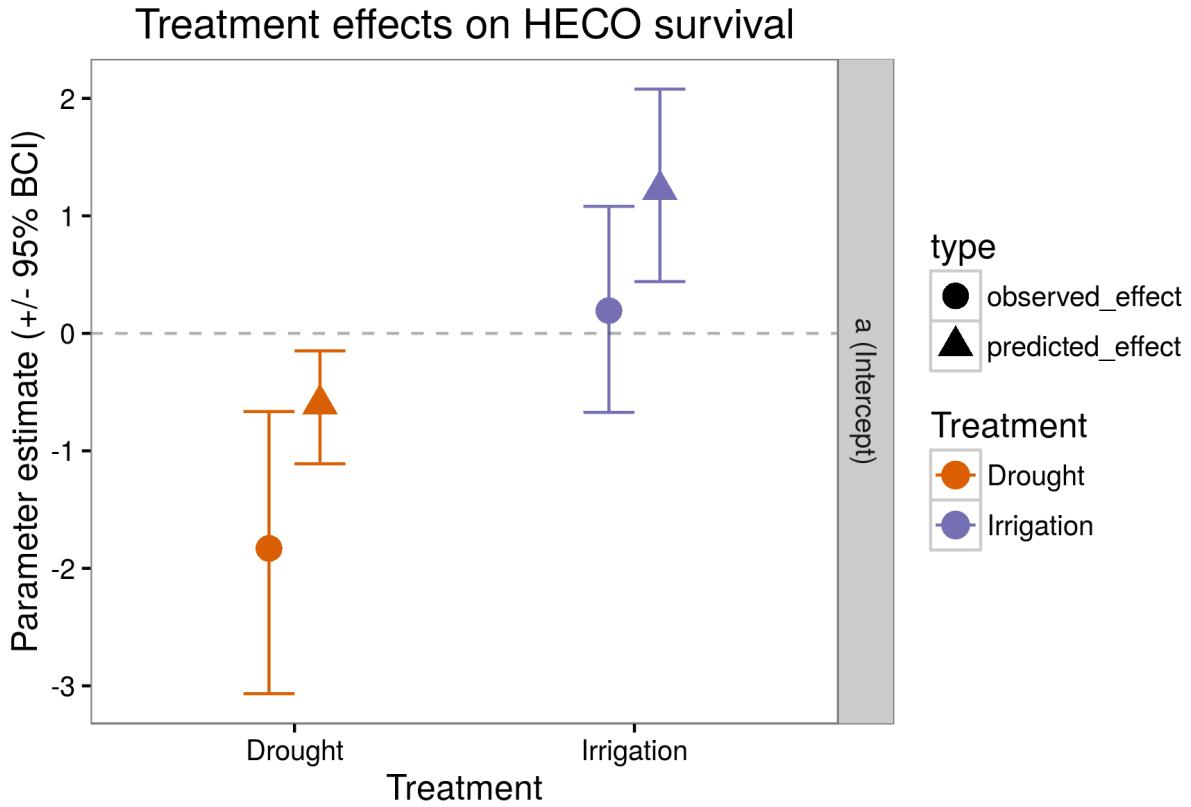


Figure A-6: Comparison of treatment effects predicted and observed for *H. comata* survival. The observed treatment effects come from the treatment model fitted to all the data including the five years of the experiment. The predicted parameters come from the climate model fitted to all years of observational data but do not include the five years of the experiment (2011 to 2016). We assessed a parameter as significant when the 95% Bayesian credible intervals did not overlap zero.

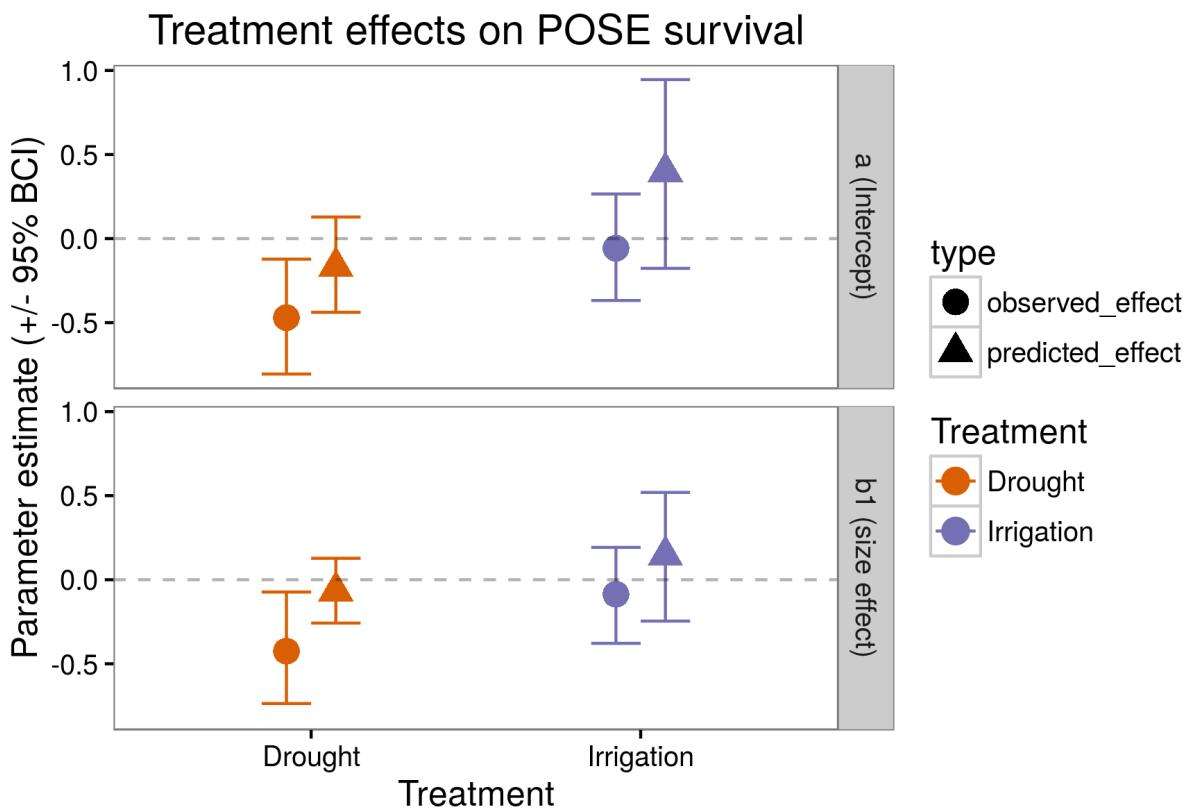


Figure A-7: Comparison of treatment effects predicted and observed for *P. secunda* survival. Upper figure shows each parameter estimate separately while the lower figure shows the effect of treatment as a function of plant size. The observed treatment effects come from the treatment model fitted to all the data including the five years of the experiment. The predicted parameters come from the climate model fitted to all years of observational data but do not include the five years of the experiment (2011 to 2016). We assessed a parameter as significant when the 95% Bayesian credible intervals did not overlap zero.

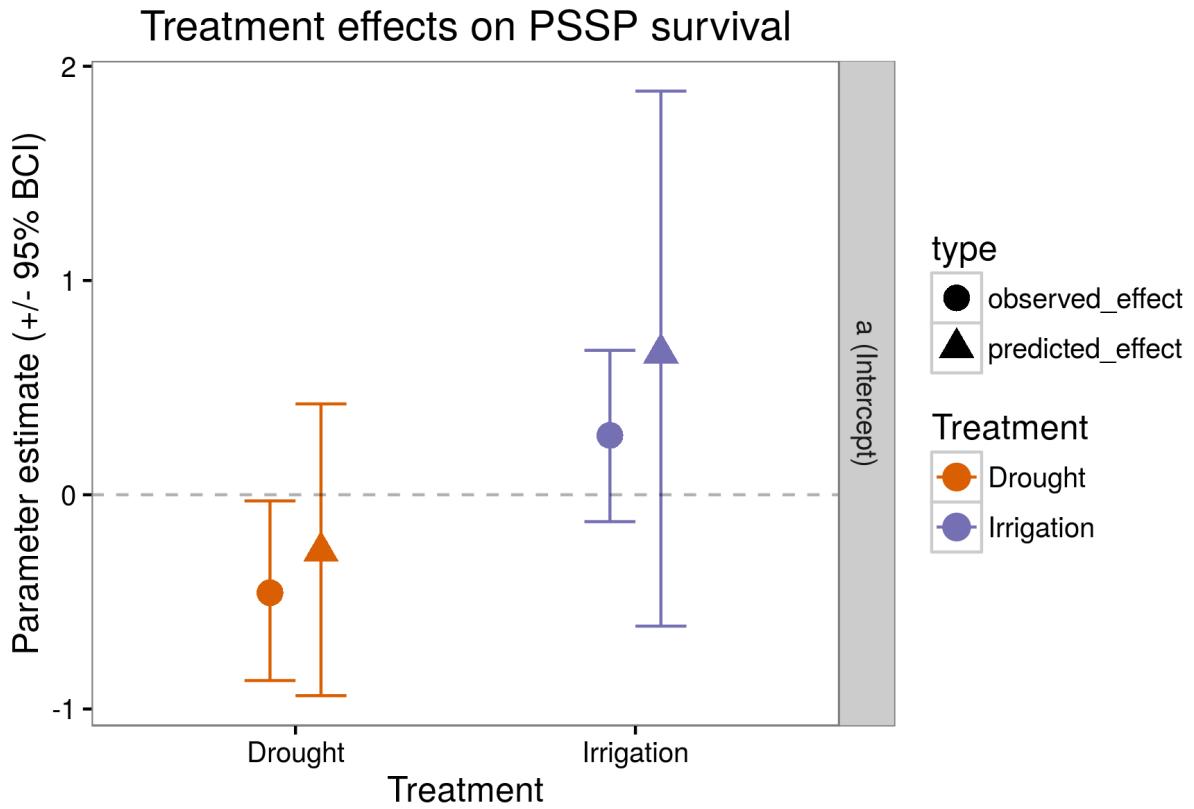


Figure A-8: Comparison of treatment effects predicted and observed for *P. spicata* survival. The observed treatment effects come from the treatment model fitted to all the data including the five years of the experiment. The predicted parameters come from the climate model fitted to all years of observational data but do not include the five years of the experiment (2011 to 2016). We assessed a parameter as significant when the 95% Bayesian credible intervals did not overlap zero.

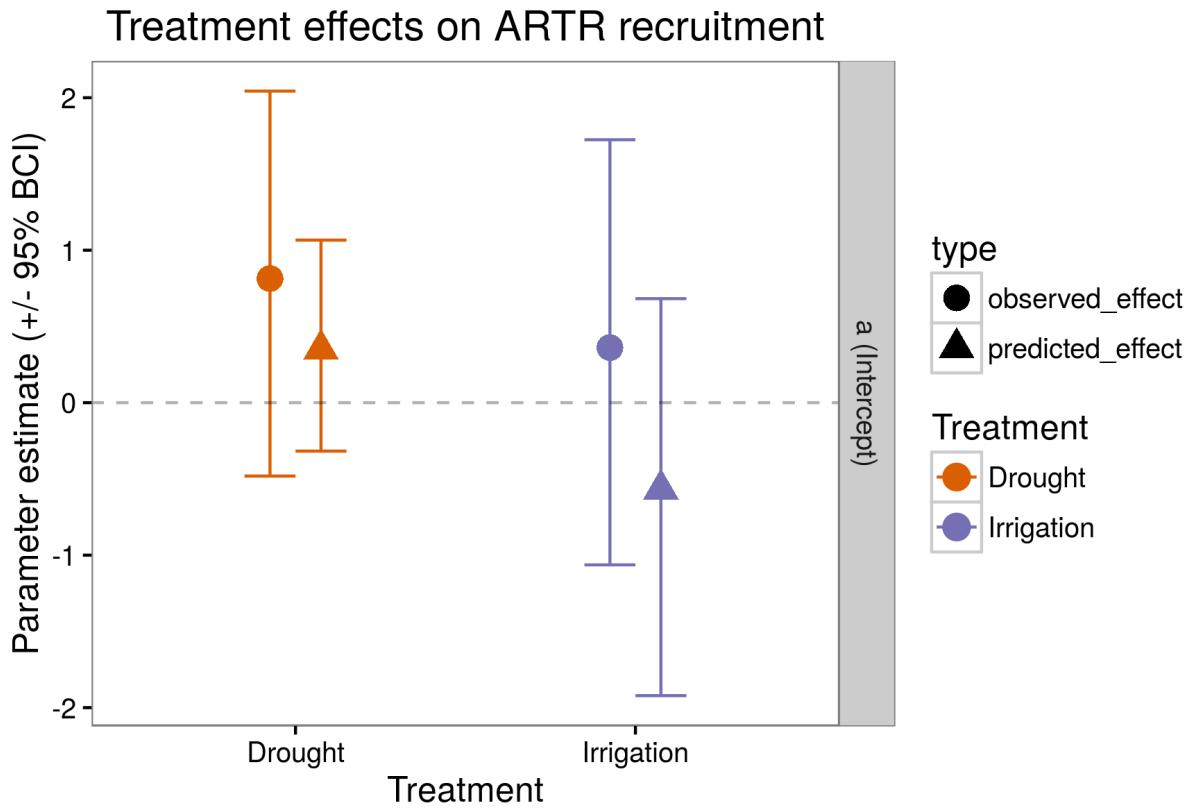


Figure A-9: Comparison of treatment effects predicted and observed for *A. tripartita* recruitment. The observed treatment effects come from the treatment model fitted to all the data including the five years of the experiment. The predicted parameters come from the climate model fitted to all years of observational data but do not include the five years of the experiment (2011 to 2016). We assessed a parameter as significant when the 95% Bayesian credible intervals did not overlap zero.

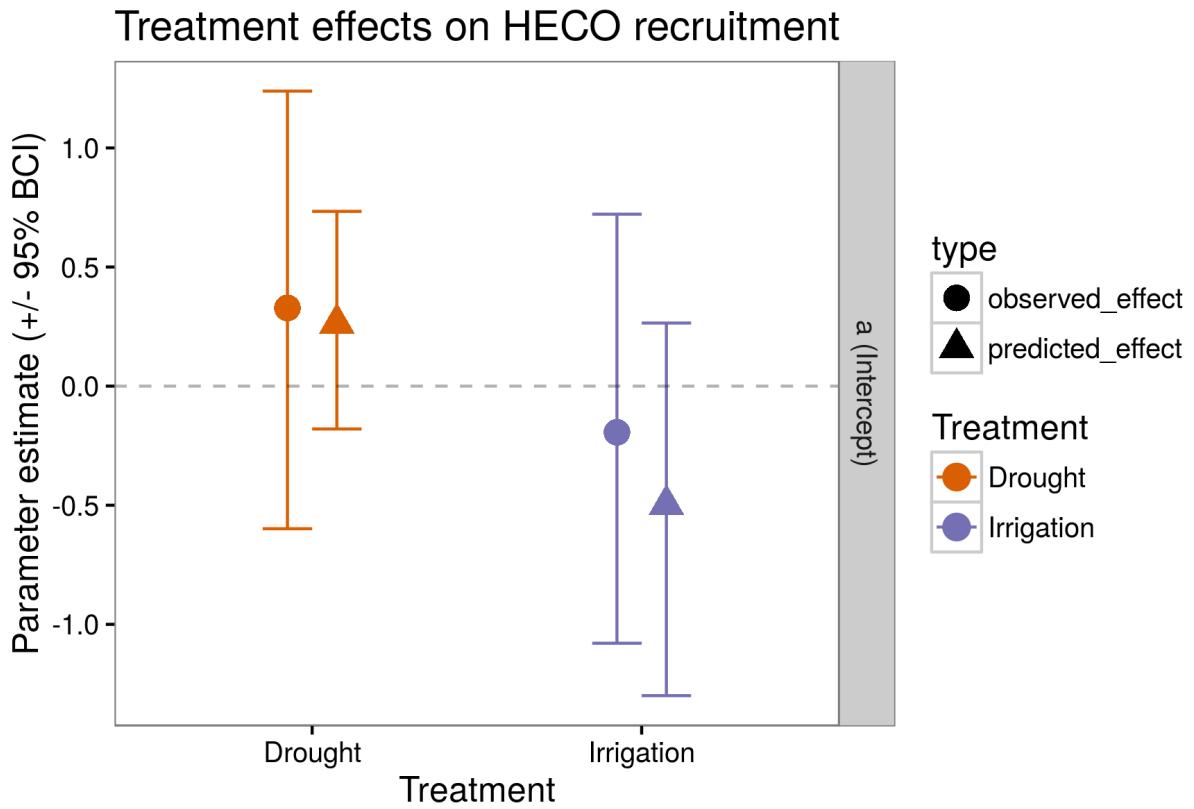


Figure A-10: Comparison of treatment effects predicted and observed for *H. comata* recruitment. The observed treatment effects come from the treatment model fitted to all the data including the five years of the experiment. The predicted parameters come from the climate model fitted to all years of observational data but do not include the five years of the experiment (2011 to 2016). We assessed a parameter as significant when the 95% Bayesian credible intervals did not overlap zero.

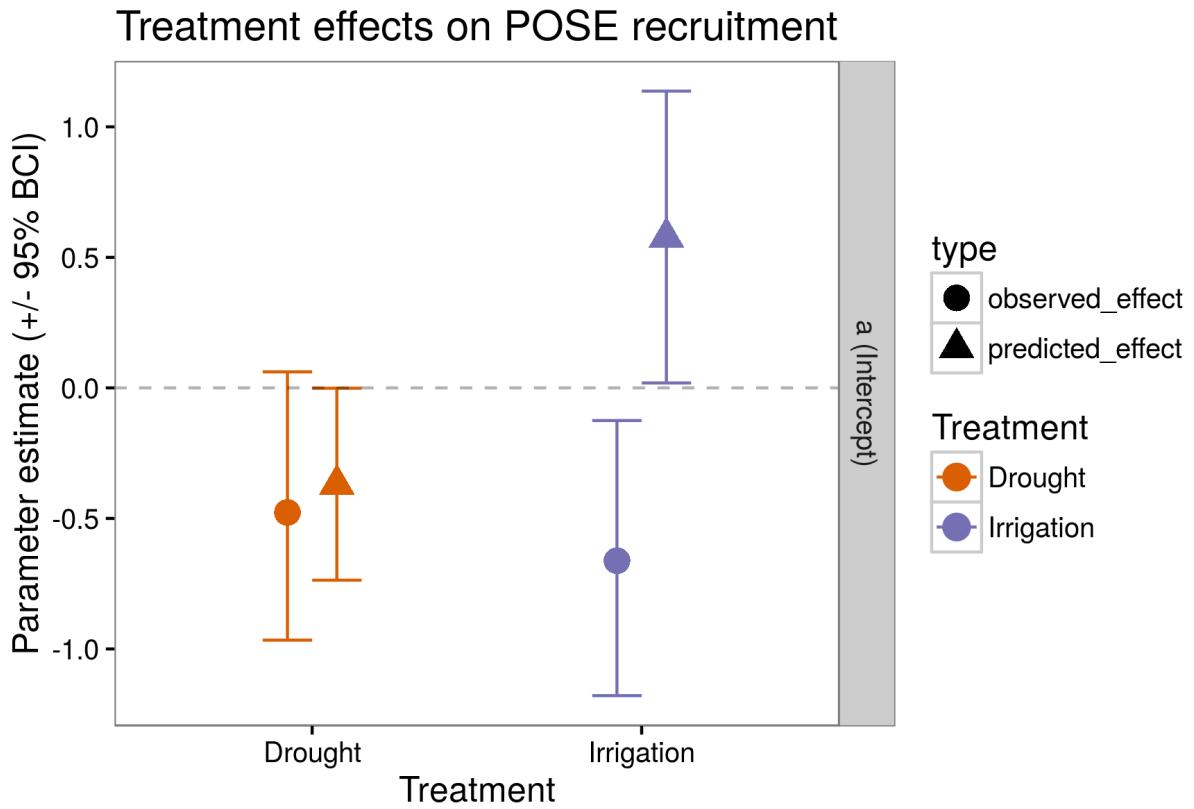


Figure A-11: Comparison of treatment effects predicted and observed for *P. secunda* recruitment. The observed treatment effects come from the treatment model fitted to all the data including the five years of the experiment. The predicted parameters come from the climate model fitted to all years of observational data but do not include the five years of the experiment (2011 to 2016). We assessed a parameter as significant when the 95% Bayesian credible intervals did not overlap zero.

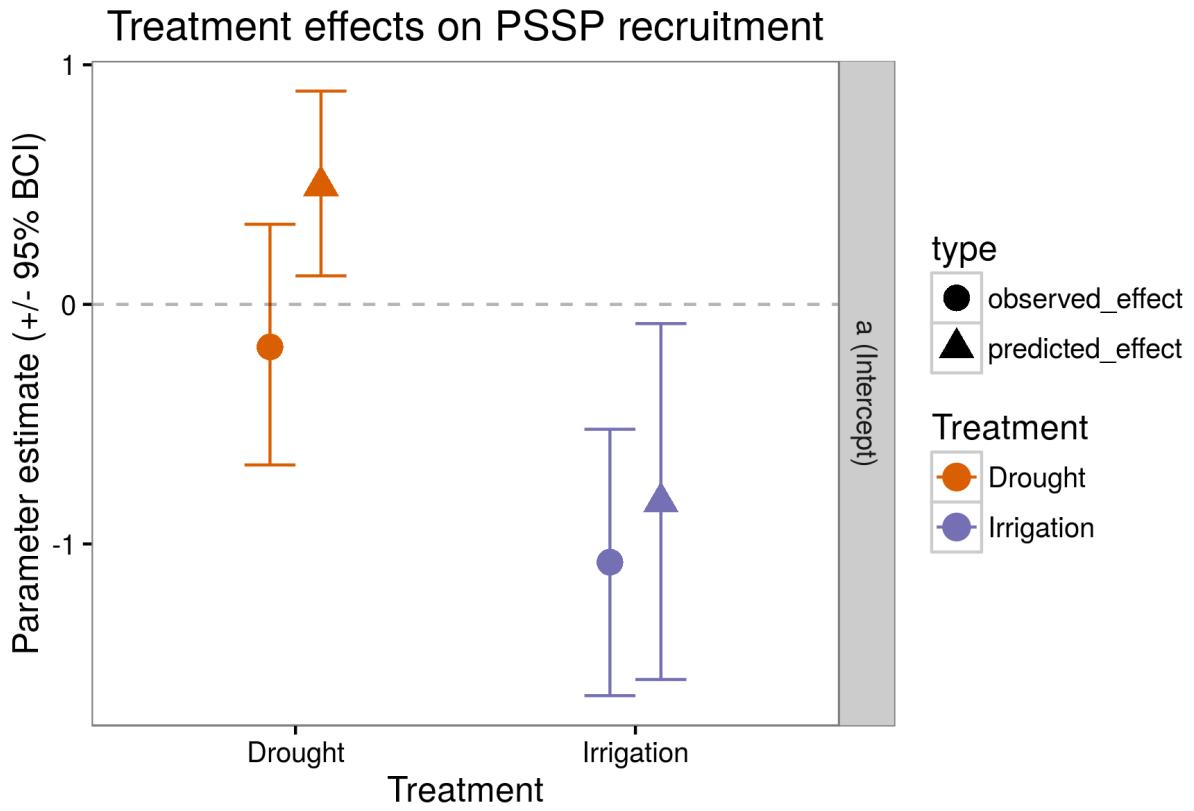


Figure A-12: Comparison of treatment effects predicted and observed for *P. spicata* recruitment. The observed treatment effects come from the treatment model fitted to all the data including the five years of the experiment. The predicted parameters come from the climate model fitted to all years of observational data but do not include the five years of the experiment (2011 to 2016). We assessed a parameter as significant when the 95% Bayesian credible intervals did not overlap zero.