Water the odds: Precipitation manipulations impact different stages of plant recruitment in a mixed-grass prairie ecosystem

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Abstract

Changes in precipitation patterns paired with exotic species invasion pose a threat to grassland biodiversity and ecosystem functions. To understand how Front Range plants will respond to projected precipitation changes, we designed an experiment to simulate spring (March-May) and summer (June-August) drought on 17 common, functionally diverse prairie plant species. Our common garden experiment was conducted in Boulder, Colorado from February 2018 to August 2018. Plants were individually sown and monitored weekly for emergence and flowering timing. Extreme precipitation significantly impacted plant survival in different life stages depending on the timing of precipitation manipulation. Spring drought decreased emergence likelihood by 54% ($p = 0.0399$) and wet spring significantly increased emergence likelihood by 169.6% ($p = 0.0416$). A wetter spring also significantly increased the likelihood of plant survival after germination when effects were aggregated across the 17 species. The transition from seed to seedling was the most pronounced bottleneck in a species reaching recruitment (becoming a mature member of a population), which suggests the need for increased care of native plants seeds during years of early drought.

Keywords: Recruitment, Drought, Front Range, Grassland, Germination, Emergence
Introduction

The prairie biome helps regulate atmospheric gas concentrations, conserves soil through erosion control and soil creation, supports pollination services and is valued at $906 Billion USD yr\(^{-1}\) globally (Daily, 1997; Costanza et al., 1997). Maintenance of plant biodiversity sustains these benefits (Forest et al., 2011) because different species contribute different ecosystem services, and functional redundancy increases resilience to disturbance (Gamfeldt et al., 2008; Lawton, 1994; Bolam et al., 2002; Tilman and Downing, 1994). Biodiversity includes not only the variation in services provided by individual plant species, but also the differences in species’ responses to environmental threats. Understanding how this diversity in responses can stabilize ecosystems is important to restoration efforts (Elmqvist et al., 2003) and will be critical to the restoration of grasslands. Climate change and invasive species threaten biodiversity, and by extension, the stability and services of contemporary ecosystems (IUCN, 2007; Dirzo and Raven, 2003). Globally, the effects of climate change will cause an increase in the frequency and severity of extreme precipitation events, like droughts (IUCN, 2007). Soils in semi-arid regions, including Colorado, are expected to become drier, which can be a consequence of both decreased rainfall and increased temperatures (Manabe et al., 2004). In Boulder, soil moisture will likely decrease because of a trend of warming summers (Lawton, 2010). When comparing climate data from the last 30 years to the previous 70, Lawton (2010) found that Boulder has been experiencing wetter springs and hotter summers (with no significant change in summer precipitation). Because summer precipitation will stay the same, but temperatures will increase, soils will be drier (Lawton, 2010: EPA, 2016). Being able to predict how plant communities will change under future climate projections will aid land managers in restoration efforts and is important as environmental degradation intensifies (Tilman, 1999). These predictions may be
possible by analyzing traits that confer differences in plant responses to environmental changes (Suding and Goldstein, 2008).

Grassland communities subjected to drought generally respond similarly (St. Clair et al., 2009): grasses will be shorter and senesce (Deléglise et al., 2015) and seed production and biomass will decrease (St. Clair et al., 2009). However, certain types of species within a grassland ecosystem can tolerate drought better than others (Potts et al., 2012). This variability may be associated with different vulnerabilities at critical life stages (James et al., 2011). Before reaching recruitment (being considered an adult in a population), a plant undergoes several transitions. Germination and emergence are the transitions from seed to seedling and are generally considered to be greatest bottleneck, or defining time, for later species contribution (James et al., 2011; Larson et al., 2015). Recruitment mechanisms and causes of failure are less well studied than later-stage plant characteristics, especially in grasslands (Fraaije et al., 2015), but could be an important window to study in order to understand community composition changes as a result of different disturbances (James et al., 2011; Larson et al., 2015).

Within the same environment, germination and emergence success is variable by species (Larson et al., 2015). In a winter-wet California system, drought increased the proportion of exotic annual grasses over native perennials (Potts et al., 2012). Typically, annual plants will emerge in higher numbers and dominate an ecosystem soon after disturbance, but perennials can outcompete and dominate long-term (Seabloom et al., 2003; Tilman, 1999).

Trait-based ecology seeks to explain community responses to environmental variability using measurable differences in species’ characteristics (Suding and Goldstein, 2008). Often, functional traits (i.e. morphological features like seed mass) are tied to shifts in community composition. However, processing traits (i.e. species’ unique demographic responses, such as
germination, recruitment, or seed production responses) mechanismically link functional traits to community-level changes in population abundances (Lavorel and Garnier, 2002). While processing traits are poorly studied, they are an important bridge between functional traits and plant community distribution (Öster and Eriksson, 2012; Larson et al., 2015). Because the period between germination and emergence is often the time of greatest plant mortality (James et al., 2011), studying emergence timing and frequency is an effective way to be able to predict community responses under future precipitation projections. The novel ecosystems that are emerging as a result of climate change and species invasion will require new restoration approaches (Seastedt et al., 2008). Identifying the most vulnerable demographic stages under novel conditions, such as invasion and extreme drought, is an important first step toward increasing recruitment success for restoration projects.

Restoration is one of the primary goals of the City of Boulder’s Open Space and Mountain Parks’ management plan (City of Boulder, 2010). Reestablishing historic plant communities is not always attainable, and land managers must thus facilitate new ecosystems that are able to function in the future despite intensifying climate change and exotic invasion intensify (Seastedt et al., 2008). If species’ recruitment patterns under different environmental conditions (i.e. wet and dry years) can be linked to species traits, one may be able to use these same traits to predict longer-term patterns of plant community response across managed lands. Predicting the impact of novel weather conditions on assemblies of native and invasive plant communities based on the knowledge of trait-based and functional group responses to changing climates is paramount to developing future restoration models (Laughlin and Hooper, 2014).

The purpose of this study is to assess how drought may differentially affect seedling germination and recruitment of co-occurring species in the xeric tallgrass prairie of Colorado’s
Front Range (Boulder, CO). To understand plant recruitment dynamics, we seeded a range of exotic and native species and manipulated seasonal precipitation over the first year of growth to explore the effects of extreme precipitation on germination timing and totals, plant survival, flowering and growth. I addressed the following questions: (1) Do plants exhibit substantially different recruitment and biomass based on precipitation variability, (2) When is recruitment failure occurring in different treatments, and (3) Can species traits (i.e. functional group or native vs. exotic) be used to explain variation in recruitment?

**Methods**

*Site Description and Study Species*

Seedling demographic data were collected under a precipitation manipulation for 17 common, functionally diverse prairie species (Table 1) in a common garden experiment in Boulder, Colorado, US (elevation 1624m, 424 mm average annual precipitation). The base of Colorado’s Front Range supports a xeric, tallgrass prairie system that hosts a unique mix of grassland and montane plant species (Marr, 1961). Seventeen species were chosen for the study to represent the functional diversity of common native and exotic plant species in the Front Range (Table 1). Seeds were locally collected and tested to control for viability.

**Table 1.** Seventeen, locally collected, plant species from Boulder Open Space were studied from seed to recruitment. Species represent the functional diversity of plants in the Front Range.

<table>
<thead>
<tr>
<th>Common Name</th>
<th>Species</th>
<th>Functional Niche</th>
</tr>
</thead>
<tbody>
<tr>
<td>Big bluestem</td>
<td><em>Andropogon gerardii</em></td>
<td>Native; Warm season, perennial grass</td>
</tr>
<tr>
<td>Prairie sagewort</td>
<td><em>Artemisia frigida</em></td>
<td>Native; Perennial woody</td>
</tr>
<tr>
<td>Smooth white aster</td>
<td><em>Aster porteri</em></td>
<td>Native; Perennial forb</td>
</tr>
<tr>
<td>Smooth brome</td>
<td><em>Bromus inermis</em></td>
<td>Exotic; C3 perennial grass</td>
</tr>
<tr>
<td>Japanese brome</td>
<td><em>Bromus japonicus</em></td>
<td>Exotic; Annual grass</td>
</tr>
<tr>
<td>Chicory</td>
<td><em>Cichorium intybus</em></td>
<td>Exotic; Perennial forb</td>
</tr>
<tr>
<td>Grass pink</td>
<td><em>Dianthus armeria</em></td>
<td>Exotic; Annual forb</td>
</tr>
<tr>
<td>Squirreltail</td>
<td><em>Elymus elymoides</em></td>
<td>Native; C3 perennial grass</td>
</tr>
<tr>
<td>Hairy false goldenaster</td>
<td><em>Heterotheca foliosa</em></td>
<td>Native; Perennial forb</td>
</tr>
<tr>
<td>Dotted blazingstar</td>
<td><em>Liatris punctata</em></td>
<td>Native; Perennial forb</td>
</tr>
<tr>
<td>Switchgrass</td>
<td><em>Panicum virgatum</em></td>
<td>Native; C4 perennial grass</td>
</tr>
<tr>
<td>Slimflower scurfpea</td>
<td><em>Psoralidium tenuiflorum</em></td>
<td>Native; Perennial legume</td>
</tr>
<tr>
<td>Species</td>
<td>Scientific Name</td>
<td>Native Status</td>
</tr>
<tr>
<td>----------------------</td>
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</tr>
<tr>
<td>Prairie coneflower</td>
<td><em>Ratibida columnifera</em></td>
<td>Native</td>
</tr>
<tr>
<td>Little bluestem</td>
<td><em>Schizocyrium scoparium</em></td>
<td>Native</td>
</tr>
<tr>
<td>Yellow salsify</td>
<td><em>Tragopogon dubius</em></td>
<td>Exotic</td>
</tr>
<tr>
<td>Blue vervain</td>
<td><em>Verbena hastata</em></td>
<td>Native</td>
</tr>
<tr>
<td>Sixweeks fescue</td>
<td><em>Vulpia octoflora</em></td>
<td>Native</td>
</tr>
</tbody>
</table>

**Experimental Design**

To follow the recruitment of individuals from seed, we hand sowed 10 seeds per species in 20 plots in February 2018 (17 species x 10 species = 170 seeds per plot). Plots were tilled, homogenized, and separated by plastic lining approximately 20 cm deep to prevent water flow between plots. Chicken wire covered the plots (approx. 20cm above the soil) to deter herbivory. Before the experiment, volumetric water content of the soil was similar across the plots (12.19% ± 1.49 to a depth of 12cm). In each plot, seeds were planted 3 cm apart in a grid (approx. 40cm x 40cm, with a buffer of approx. 0.6m from the plot edge) in a completely randomized order. To aid in location and identification, we glued each seed to a color-coded paper clip (non-toxic, water soluble glue). After the study, in September, we tested for the effect of glue by planting 10 individuals of each small seeded species glued to paperclips and 10 individuals not glued to paperclips. Nutrient-free water was added to match soil moisture content with the soil moisture of the week where most plants germinated in the spring.

To understand how seedling recruitment dynamics respond to shifts in spring and summer rainfall patterns, we assigned plots to one of the following five treatments from March through August: (1) spring drought (2) summer drought (3) spring water surplus (4) summer water surplus and (5) control (ambient rainfall) (see ‘Precipitation Manipulation’). Four
replicates of each treatment were arranged in a block design (Figure 1).

![Figure 1. Plots were arranged to distribute treatments throughout the common garden. Different colors represent different blocks that contain one replicate of each treatment type. The four blocks of five treatments make up the 20 experimental plots.](image)

*Precipitation Manipulation*

To implement treatments, we constructed rain shelters that fully excluded and collected precipitation. Spring precipitation manipulations ran from March – June, and summer treatments ran from June – August. In the spring, spring drought plots received 50% of precipitation and spring wet plots received 150% of precipitation. In the same time period, summer manipulation plots and control plots received ambient rainfall. In the summer (June – August), summer drought plots received 50% of rainfall and summer wet plots received 150% of ambient rainfall.

The structures reduced light by 23.3% from ambient conditions (under shelter: $31.09 \pm 1.97 \, \mu\text{mol m}^{-2}\text{s}^{-1}$; ambient: $25.86 \pm 1.23 \, \mu\text{mol m}^{-2}\text{s}^{-1}$) and increased temperature by 20.2% (under shelter: $31.1 \pm 3.65 \, ^\circ\text{C}$; ambient: $26.0 \pm 1.62 \, ^\circ\text{C}$) (measured at mid-day on a clear day in April). To minimize confounding effects, we only put rain shelters on when precipitation was forecasted, and we re-distributed water within 24 hours of the end of each storm. Water collected from the four structures was pooled and re-distributed evenly across the eight experimental plots. If a structure collected $>30\%$ less water than the average of the other structures (e.g., due to an external leak), nutrient-free water was used to supplement the pooled water supply. Large rain events were re-distributed over longer periods of time—no more than 5 liters of water were
added to a plot within three hours. Snow that persisted for more than 24 hours was re-distributed as snow and otherwise added as liquid water. To evaluate treatment effects on soil moisture, we collected volumetric water content (VWC, %) periodically to a depth of 12 cm throughout the seven months, including before and after most rain events (n=24 sampling dates; Campbell Scientific Hydrosense II handheld soil moisture sensor). At each sampling date, we measured VWC for each plot as the average of three sub-samples within 5 cm of the planted seeds. Rainfall was averaged between three rain gauges placed in separate locations near the experiment sight. In storms where there was too little rain to be detected by our gauges, we used the CU-Boulder Weather Station recordings.

*Life-History Data Collection*

We conducted a weekly census of the plants from March through August 2018 and recorded germination date, flowering date and death date (if applicable). In mid-June, most individuals of *B. japonicus* and *T. dubius* had begun to flower and dominate the canopy – growing up to 18 cm in diameter in some cases and blocking neighboring individuals. To reduce overwhelming effects of interspecific competition, we randomly pulled individuals of these two species to until four remained per plot. To account for possible plot differences in interspecific competition, we recorded total vegetative cover (percent, by visual estimate [single observer]) at the end of the early treatment and twice during the late treatment. At the end of the experiment, we also harvested plants to estimate above-ground biomass for each species. Because of the vast number of individuals (60+ individuals per some species), we pooled individuals of a species at the plot level if there plants in at least three of the replicate plots per treatment. Otherwise, plants were harvested and weighed individually. All plants less than 50% dry by the end of the growing
season were harvested for aboveground biomass and dried at 60 °C for at least 48 hours before being weighed.

Statistical Analysis

To evaluate the effects on soil moisture, we performed a repeated measure ANOVA for the spring season and summer season. To test for possible treatment differences in interspecific competition, we measured percent cover three times throughout the study period (end of spring treatment, mid-summer and experiment end).

Generalized linear mixed models were used to assess the effect of precipitation treatment on germination and survival rates. We used a binomial link function with a random slope and intercept model so that all groups, in this case treatments, could have different intercepts and effect sizes. We included precipitation treatment as a fixed effect, and species and block were treated as random effects. When species was included as a fixed effect, to test treatment and species interactions, the models could not converge due to the large number of interactions. Because we were unable to isolate species and treatment interaction in the model that contained all species, we also conducted generalized linear mixed models for each individual species where more than five individuals emerged to compare emergence and survival responses to precipitation including precipitation treatment as a fixed effect and block as a random effect. We used the Kaplan-Meier survivorship model to predict the timing of different life-history traits (i.e. death and flowering time).

Results

Soil Moisture

Treatment had a significant effect on soil moisture in the spring but not in the summer (Figure 2). The spring drought treatment was significantly drier than the control (p = 9.6 x 10^-6),
summer wet treatment (p = 4.0 x 10^{-6}), summer drought treatment (p = 9.7 T x 10^{-6}) and spring wet treatment (p = 4.9 x 10^{-9}). As expected, the summer treatments were statistically equivalent to the control before June 1, when the treatments switched. The spring wet treatment was not different from the control or the summer treatments. After June 1, there was no effect of treatment on soil moisture.

![Soil Moisture by Treatment and Precipitation (February - August)](image)

**Figure 2.** Precipitation and volumetric water content from March – August. The bars show precipitation in cm and the lines show volumetric water content by treatment. The dashed line shows the date that the treatments were switched from spring to summer (June 1, 2018).

*Emergence Response to Treatments*

Of the 3400 seeds planted, 20.7% emerged, and 66% of the emerged plants survived. Survivorship was defined as any plant that was alive by the end of the study or that flowered and died by the end of the study. The average emergence day was April 12 (± 0.58; median = April 8) and the most common emergence day was April 8 (Figure 3). The first individuals to germinate were *B. japonicus* on March 17.
Plants were 54% less likely to germinate in the spring drought treatment compared to the control ($p = 0.0399$), and plants were 169.6% more likely to germinate in the spring wet treatment compared to the control ($p = 0.0416$) (Figure 4). Of the 698 plants that emerged, 611 (87.5%) emerged before the summer treatments were started on June 1, 2018. Only plants that emerged before the start of the summer treatments were considered in the emergence analyses, and the summer treatments were combined with the control for emergence before June 1.
Figure 4. Percent emergence of all species based on treatment. Different letters represent significant differences in the likelihood of emerged based on the mixed generalized linear model where species and block were random effects and treatment was a fixed effect.

Emergence was significantly lower in the spring and summer drought treatments for *E. elymoides* (Figure 5). Emergence was also significantly lower for *L. punctata* in the spring drought treatment, but treatment did not affect emergence of any other species when analyzed individually using a generalized linear model (Figure 5). *Elymus elymoides* emergence was 38% less likely in the spring drought treatment compared to the control (*p* = 0.0156) (Figure 5). *Liatris punctata* was 39% less likely to emerge in the spring drought treatment compared to the control (*p* = 0.0152). Two other native species, *P. virgatum* and *S. scoparium*, emerged significantly more in the spring wet plots than the control. *Panicum virgatum* was 276% more likely to emerge under spring wet conditions than the control (*p* = 0.0392), and *S. scoparium* was 319% more likely to emerge in the spring wet treatment than the control (*p* = 0.0208) (Figure 5). Emergence of *B. japonicus*, *B. inermis* and *T. dubius* were unaffected by treatment, and had sufficient seedlings to be confident in the analysis (Figure 5). *A. gerardi*, *C. intybus*, *H. foliosa*,...
*P. tenuiflorum* and *V. octoflora* did not show significant effects of treatment on emergence, but it could be that the low number of seedlings did not provide enough statistical power to show differences in emergence patterns (Figure 5). Five of the 17 species (*A. frigita, A. porteri, D. armeria, R. columnifera,* and *V. hastata*) did not emerge in some or all of the treatments and therefore were not analyzed as individual species.
Figure 5. Emergence percent by treatment and species for species with seedlings in at least two treatments. Letters represent significant differences (p < 0.05) in percent emergence between the designated treatment and the control.
Treatment Effect on Survival

Seventy percent of plants that emerged survived to the end of the experiment or flowered and died by the end of the experiment (Figure 6). Sixty-three percent of plants in the control survived; 69% of spring drought plants survived; 75% of spring wet plants survived; 71% of summer drought plants survived, and 74% of the summer wet plants survived (Figure 6). Survival was 182% more likely in the spring wet treatment compared to the control (0.0235). Plants were 166% more likely to survive in the summer wet treatment compared to the control, but the difference was not significant (0.058). All other treatments did not differ significantly from the control (Figure 6). July 20 was the most common day for plants to die, which aligns with one of the driest weeks of the experiment by soil moisture (Figures 1, 7).

**Figure 6.** Percent survived of all species based on treatment for plants that germinated. Different letters represent significant differences in the likelihood of emerged based on the mixed generalized linear model where species and block were random effects and treatment was a fixed effect.
Figure 7. Death day in Julian Day across all species and treatments from March to August. Plants that were pulled by us or eaten by a rodent are not included in this figure.

_Bromus inermis_ survived significantly more in the spring wet plots than the control (p = 0.0176) and 100% of individuals survived in the summer wet treatment (Figure 8). There was not a significant effect of treatment on survival for _T. dubius_ (Figure 8).

The generalized linear model had difficulty establishing significance for species where 100% of plants in a treatment survived or 0% of plants in a treatment survived. For instance, all _A. gerardi_ individuals survived in the spring drought treatment and the summer wet treatment, compared to ~30% (± 33%) survival in the control, but there was not a significant difference in survival, according to the model’s calculations (Figure 8). All _C. intybus_ individuals survived in the control and early drought plots, and 50% survived in the other three treatments (Figure 8). _Heterotheca foliosa_ had 100% survival in the control, spring drought and summer drought treatments; there was not a significant difference in survival by treatment for _H. foliosa_ (Figure 8). Under spring drought and summer wet, 100% of _P. virgatum_ survived, but the model did not detect significant differences from the control, where 50% (± 29%) survived (Figure 8).
was also 100% survival of *S. scoparium* in the early drought plots, but no significant differences between the control (∼60% ± 24% survival) and other treatments (Figure 8).

In other instances, it is possible that no significant differences were detected due to the low number of replicates. *Bromus japonicus, E. elymoides* and *L. punctata* likely lacked sufficient replication to generate meaningful analysis. No significant differences were detected for survival of *B. japonicus, E. elymoides* and *L. punctate*. Survival analysis was not conducted for *P. tenuiflorum* because all individuals died before flowering or reaching the end of the experiment. Five other species (*A. frigita, A. porteri, D. armeria, R. columnifera, and V. hastata*) did not emerge in some or all of the treatments and therefore were not analyzed for survival as individual species.
Figure 8. Survival fraction by treatment and species for species with more than one surviving plant. Letters represent significant differences (p < 0.05) in survival between the designated treatment and the control based on the generalized linear model.
There were no differences in dry weight of aboveground biomass for *E. elymoides*, *H. foliosa* or *L. punctata* at the end of the study, based on treatment. Exotic plants have not been analyzed for dry mass differences.

**Survivorship Curves**

There is no impact of treatment on the likelihood of survival at a certain time point (Figure 9). Beyond 150 days after germination, plants in all treatments have over a 50% chance of survival. The study terminated before any individual could reach 200 days old.

![Survivorship curve](image)

**Figure 9.** Kaplan-Meier survival curve based on treatment. Time in number of days since germination and not related to Julian Day of the year.

The functional group of a plant did have a significant impact on its likelihood of survival. Perennial grasses have a 34% lower instantaneous hazard of death than annual grasses (*p* = 0.049). Survival for annual grasses was categorized by completing the life cycle before the study’s termination (i.e. if a plant flowered and died within the timeframe of the study, it was counted as “survived”). Perennial forbs were at a 41% lower risk for instantaneous death than annual grasses (*p* = 0.0082). Perennial grasses were no more likely to survive than perennial
forbs across the timespan of the study (Figure 10). Legumes were significantly less likely to survive than any other functional groups. *P. tenuiflorum* was the only legume included in the study, and the six individuals that germinated died, without flowering.

![Kaplan-Meier survival curve based on species' functional groups. Time in number of days since germination and not related to Julian Day of the year.](image)

**Figure 10.** Kaplan-Meier survival curve based on species’ functional groups. Time in number of days since germination and not related to Julian Day of the year.

There is a 63% higher instantaneous hazard of death as a native plant compared to an exotic plant (*p* = 0.021), and native plants die earlier in their life-spans than exotics (Figure 11).
Figure 11. Kaplan-Meier survival curve based on native versus exotic origin. Time in number of days since germination and not related to Julian Day of the year.

Community Composition

Of the 3400 seeds sowed in February, 465 plants reached recruitment (~14% survival). Thirteen percent of native seeds emerged, and 71% survived. Comparatively, 37% of exotics emerged, and 69% survived. After accounting for the number of native versus invasive species added, this means that the community at the end of the study consisted of 53% exotic species and 47% native species, despite beginning the experiment with over two times more native seeds than exotic seeds. By treatment and origin, the most successful plants were the exotics in the spring wet treatment (33% of seeds reached recruitment) and the least successful plants were the natives in the spring drought treatment (6.5% of seeds reached recruitment). Exotic and native plants exhibited similar responses to changes in precipitation (Figure 12). This recruitment analysis was not conducted to determine final populations based on functional group or species.
Influence of Seed Mass on Life History Traits

Larger seed mass was correlated with higher emergence in the control plots ($p = 0.00512$) and in the spring drought plots ($p = 0.00737$) before June 1 (Figure 14). Early drought has the same impact on plant emergence regardless of seed mass (Figure 13). Seed size also did not impact the likelihood of emergence in the spring wet treatment. Seed mass was not related to survival in any treatment.

Figure 12. The percent of seeds that reached recruitment by origin (exotic/native) and treatment.

Figure 13. The influence of seed mass on percent emergence of species in the study that had at least one individual emerge in each treatment.
Figure 14. The difference in the logarithm of emergence compared to seed mass to determine if seed mass influenced emergence success under spring drought conditions.

Discussion

The experiment answered the three initial questions. Precipitation variability significantly impacted some stages of recruitment but did not affect aboveground biomass. Emergence was significantly lower in the spring drought treatment compared to the control and was significantly higher in the spring wet treatment compared to the control (Figure 6). Natives were the only plants to exhibit significant differences in emergence due to changes in precipitation (Figure 8). Typically, native prairie grasses have a tolerance to drought (Knapp, 1985), but it is likely that the grasses in our study were negatively affected by drought because we studied early life-history trait responses, rather than the responses of established prairie grasses to drought. This means that in the prairie, where recruitment failure is less studied because plants are generally long-lived, we must still consider the additional vulnerable stage of emergence when designing land management protocols. Based on these results of this study, it is still unclear if an environmental
signal during drought delayed the germination of seeds until a more favorable year or if seeds germinated and died before emergence. To understand the exact time of recruitment failure in this system it would be helpful to know if seeds that did not emerge in one year may still be viable in subsequent years. Other species in the study, including exotic grasses and forbs, were unaffected by precipitation differences in the spring.

Unlike other studies (Deléglise et al., 2015; St. Clair et al., 2009), we did not detect vegetative differences in drought plots compared to other plots, but it could be that differences in belowground biomass are more pronounced and should be studied in future drought studies (Fry et al., 2018). Although some species did not show treatment effects through differences in emergence, survival or aboveground biomass, it is possible that other subtler features, such as the nutritional value of the vegetation may have changed (Deléglise et al., 2015). In Boulder, where Open Space land is grazed, changes in nutritional content of grasses could be important topics of study in the future.

Our findings support previous work that indicate recruitment failure is most common in the transition from seed to seedling and that emergence the most significant determinant of future community composition (James et al., 2011; Fraaije et al., 2015). Twenty-seven percent of our seeds germinated and emerged successfully this season. Once emerged, 70% of plants survived. Summer treatments did not significantly affect any stage of recruitment (emergence or survival to adulthood). It could have been hard to see summer effects on emergence or survival if the greatest bottleneck (seed to seedling) occurred in the spring (James et al., 2011; Larson et al., 2015). Once plants reached emerged, their survival was the same regardless of native or exotic origin, which has been observed previously (Seabloom et al., 2003). If land managers are able to suppress exotic seedlings and increase native survival at the beginning of their life cycle (during
the transition from seed to seedling), the established natives might be able to sustain their populations in future years regardless of disturbance.

It is possible that exotics emerge in higher percentages because they are taking advantage of different temporal windows than natives (Gloria et al., 2016). Our study supported the idea that some “super invaders” can establish and survive better than natives during natural disturbance (Daehler 2003; Potts et al., 2015). Our study provides evidence that adding water in the spring will help the exotics and natives (Figure 12). If this is the case, then the increasingly wetter winters in the Front Range (Lawton, 2010) could mean that exotics may have an increased competitive advantage in the future.

Regardless of origin (native or exotic), we found that perennial grasses and forbs are more likely to live to recruitment than annuals. We did not find a relationship between seed mass and germination or survival responses in different treatments.

Novel ecosystems are forcing land managers to explore innovative restoration approaches (Seastedt et al., 2008), and understanding how native and exotic species will respond to projected, future climatic conditions will increase restoration efficacy. If managers seed Open Space lands, native seeds should be watered, especially in years of drought, to significantly increase native recruitment. To circumvent the vulnerable stage of emergence, natives also could be planted as seedlings because we found that prairie plants were not significantly impacted by drought once emerged (Knapp, 1985). We were able to answer our study questions and determine that recruitment failure was triggered by drought during emergence and that some functional traits (i.e. annual versus perennial) can be linked to general survival patterns in a Colorado prairie.
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