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MADDIE NOLAN

The Impact of Drought and Pocket Gophers on Restored Native Perennial Bunchgrasses in California

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Abstract

Interactions between native animals and plants are likely to have large impacts on the success of restoration projects, however, interactions are understudied. For example, *Thomomys bottae* (valley pocket gopher) is a native rodent that is commonly found in grassland ecosystems in California and is known to have a large impact on the structure of these communities. To improve future restoration success, it is important to understand how valley pocket gophers impact restored grassland plants. Extreme droughts that are predicted to increase in the future may also affect valley gopher activity. We sought to explore the interactive impacts of valley pocket gophers and drought on restored *Stipa pulchra* (purple needlegrass) by comparing how gopher activity and different watering treatments impacted the growth and reproduction of purple needlegrass in a field experiment. We found that valley pocket gophers have a significant negative impact on the growth and reproduction of purple needlegrass, especially during dry years. This suggests that valley pocket gopher activity will be a larger problem for restoration during dry years, and during these years, damage could be minimized by caging sensitive plants or watering seedlings. Our results highlight the importance of including animal effects into restoration planning to improve plant establishment rates and increase the overall success of restoration efforts.

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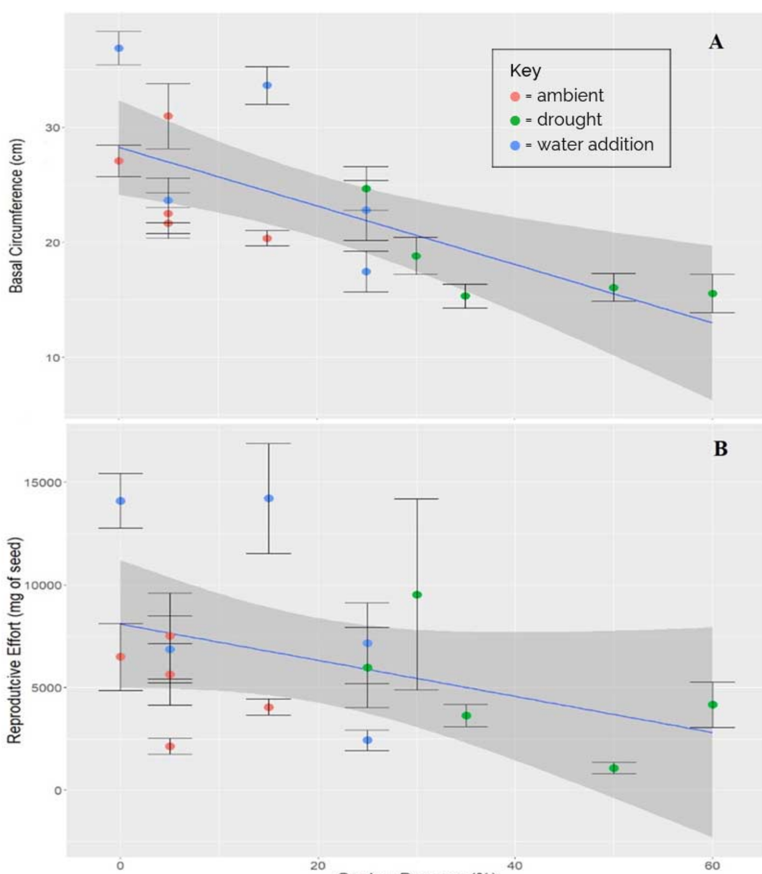

Figure 1. The impact of gopher disturbance on the basal circumference (A) and reproductive effort (B) of *S. pulchra*. Basal circumference was measured at the base of each bunch and the reproductive effort was the total seed mass produced by each plant. The line represents a multiple linear regression including watering treatment and the grey shaded area is the 95% confidence interval.

Introduction

Grasslands cover approximately 17% of California with most of this area dominated by exotic annual grasses (Huenneke 1989). Many native species that were once widespread are now typically found in isolated pockets and thinly scattered among dense exotic annual grasses (D'Antonio *et al.* 2007). These exotic-dominated grasslands also tend to persist rather than convert back to perennial communities (D'Antonio and Vitousek 1992, Stromberg and Griffin 1996, Seabloom *et al.* 2003), suggesting that active restoration is needed to reestablish native grassland communities. The state grass of California, purple needlegrass, is one of the most commonly targeted species in restoration. Purple needlegrass, and some other perennial grasses, have been the focus in grassland restoration for two main reasons. First, individuals can survive for hundreds of years (Hamilton *et al.* 2002), which makes them more likely to be persistent and stable through time compared to annual species. Second, perennial grasses form the structural basis for native grassland communities (Stromberg *et al.* 2007, Molinari and D'Antonio 2013). Therefore, it is important to explore what ecological factors can promote or impede the establishment, growth, and reproduction of this important grassland species. Interactions between native animals and restored plant communities are likely to have large impacts on the success of restoration projects; however, interactions between the two have been historically understudied in restoration ecology. Animals are also often excluded from restoration planning because it is assumed that by restoring the structure of the plant communities, the restored community will be recolonized or be more amenable to recolonization by native fauna (i.e. field of dreams hypothesis

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Hilderbrand *et al.* 2005, Hale and Swearer 2017). While there has been a steady uptick in published work on animals in restoration since the 1970s (Majer 1990), often the focus is on monitoring animals as opposed to exploring how they impact and affect ecosystem functions (Majer 2009). Relationships between animals and plant communities in California grasslands could be especially helpful in shedding light on why grassland restoration efforts often fail to successfully establish native plants.

The valley pocket gopher is an herbivorous rodent native to California with a range that extends from the southern Cascades mountains to northern Mexico (Álvarez-Castañeda 2010). Valley pocket gophers live in grassland ecosystems that were historically composed of perennial grasses such as purple needlegrass, but now tend to be dominated by exotic European annual grasses (Stromberg and Griffin 1996). Most of the year, the diet of valley pocket gophers is composed of up to 70% plant shoots (Burton and Black 1978). The removal of plants by gophers, in turn, can have a large impact on the survival of newly planted grass seedlings in a restoration project. Previous exclosure studies have shown that valley pocket gophers limit both forb abundance and community biodiversity in grassland ecosystems (Cox and Hunt 1992). Pocket gophers tend to favor feeding locations with the greatest floral biomass, reducing vegetation by over one-third in areas located above active burrows (Reichman and Smith 1985). This is particularly concerning for ecosystem restoration because if pocket gophers decrease the survival of plants that have been planted during a restoration project, this could negatively impact the long-term outlook for projects that are near large populations of gophers.

It is also important to understand how native animals impact restoration projects because these interactions are likely to interact with the effects of climate change. Precipitation is expected to be the largest driver of change in California grassland communities in the future (Dukes and Shaw 2007, Carter and Blair 2012, Harrison *et al.* 2015), becoming more variable with a greater likelihood of severe weather events such as droughts (AghaKouchak *et al.* 2014). Prior studies have found surface access-tunnel production by gophers to be uncorrelated with temperature or precipitation (Cox and Hunt 1992), but we have seen evidence of increased activity during dry years in previous experiments (D'Antonio unpublished). In addition, research on valley pocket gophers in California grasslands has demonstrated that gophers can promote exotic annual species (Seabloom and Richards 2003) and decrease the growth of native perennial bunchgrasses through their foraging activity (Stromberg and Griffin 1996, Watts 2010). However, it is unclear how these impacts on exotic and native plants will be affected by drought. Our goals were to understand how water availability impacted gopher activity and how both affect restored purple needlegrass communities. We were specifically interested in understanding how drought and gophers affected purple needlegrass seedlings that had been transplanted into the field, as opposed to populations started from seed. To accomplish this, we manipulated water availability for adjacent restored grassland plots over three years. We measured individual basal circumference and total seed weight of purple needlegrass as proxies for biomass and reproductive output, respectively. After three years, we recorded the amount of gopher disturbance in each plot as a function of total coverage. This field experiment was conducted to answer (1) how water availability in a restored grassland affected gopher activity, and (2) how gopher activity impacts the growth and reproductive output of purple needlegrass that have been transplanted into the field. These metrics are vital for creating a more accurate model for restoration planning in grassland ecosystems, thereby helping to inform

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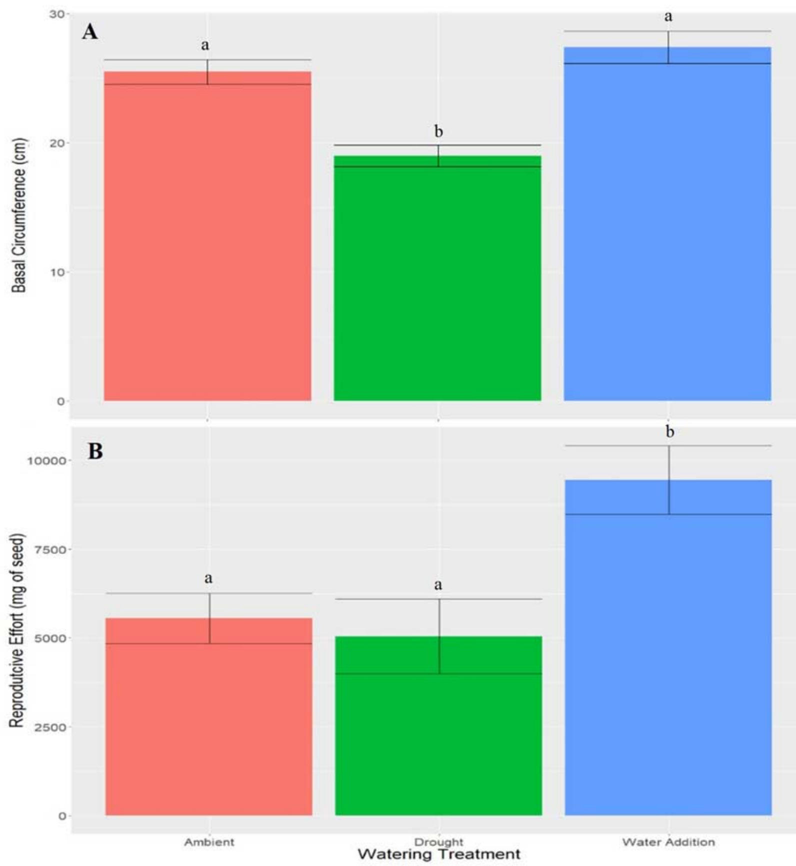

Figure 2. The impact of watering treatment on the basal circumference (A) and reproductive effort (B) of *S. pulchra*. The ambient treatment was the control, the drought treatment received a 50% reduction in precipitation, and the water addition treatment received an additional 4 weeks of water at the end of the growing season. Error bars indicate ± SE with letters indicating significant differences as measured by an Analysis of Variance.

restoration planners on strategies to mitigate potential losses to pocket gopher damage in future projects.

Experimental Design

Study Area

Our work was conducted in the Santa Ynez Valley at the Sedgwick Reserve, a 2,358-hectare reserve managed by the University of California (https://sedgwick.nrs.ucsb.edu/). The Santa Ynez Valley is located 35 miles NE of Santa Barbara between the Santa Ynez and San Rafael mountain ranges. The region has a Mediterranean climate with hot, dry summers and cool, wet winters. The majority of the mean annual precipitation (400 mm) falls between October and April, with the rest of the year periodically experiencing seasonal summer fog with little to no rainfall.

Valley Pocket Gopher

The valley pocket gopher is an herbivorous rodent native to California (Álvarez-Castañeda 2010) and tends to live in grassland ecosystems. The diet of pocket gophers is composed primarily of plant shoots (Burton and Black 1978), and they time their reproductive activity to when forb and grass shoots are most available in the spring (Hunt 1992). Pocket gophers prefer to feed on plants from underground tunnels by pulling down the entire plant into the burrow, but individuals also feed on plants outside of their burrows. Pocket gophers are known for their claw-driven burrowing habits, with the overlying vegetation of active burrows reduced by up to two-thirds of the original coverage (Reichman and Smith 1985).

Experimental Plots

Our experimental plots were located in an exotic grassland dominated by wild oat (*Avena fatua*) and Ripgut brome (*Bromus diandrus*), with native grassland species composing less than 0.01% of total biomass and plot coverage (D'Antonio unpublished). Prior to initiating watering treatments, all plots received an identical restoration treatment that consisted of exotic species removal, the addition of native grass seedlings, and maintenance weeding throughout the experiment. In 2017, we cleared all exotic biomass from fifteen 4x4m plots and scraped the top 5 cm of soil off to remove the seed bank which was dominated by wild oat seeds. Each plot had a 0.5m buffer with a 3x3m core that contained the experiment. On January 21, 2017, 12 purple needlegrass seedlings were transplanted into each plot. At the time of planting, all seedlings were approximately 4 months old and had been germinated and grown in the biology greenhouses at the University of California, Santa Barbara. After the seedlings had been transplanted, all plots were watered that day and one week later. After this initial watering, the amount of water received by the seedlings was dictated by their watering treatment. We randomly assigned one of three different watering treatments to each plot. The watering treatments were 1) a drought treatment, 2) a water addition treatment that had an extended growing season, and 3) a control treatment that received ambient rainfall. To implement the drought treatment, we erected rainout shelters that passively reduced precipitation events by 50%. Each shelter was built according to the specifications laid out by the international drought experiment (https://wp.natsci.colostate.edu/droughtnet/). Plots were also trenched down to 50 cm and a plastic shield installed to prevent lateral subsurface flow into the plots. For the water addition treatment, plots were watered biweekly (starting 4/17 in 2019, 4/11 in 2018 and 4/23 in 2019) at a rate of 6.7 L/m^2 until the end of May (ending 5/29 in 2017, 5/23 in 2018, and 5/23 in 2019). Water was not manipulated in ambient plots. Each watering treatment was replicated 5 times. Exotic species were continuously weeded from the 4x4m plots during the

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winter months in the 2016/2017 and 2018/2019 growing seasons. Exotic species were only weeded once in the 2018/2019 growing season.

Response Metrics and Analysis

In May of each year, we surveyed the planted purple needlegrass individuals. In all three growing seasons, we measured the basal circumference and the number of flowering culms. Beginning in 2018, we collected 3 flowering culms and 10 seeds from each plant when available. In 2019, we also harvested the above-ground biomass for each plant. During this annual survey, we also surveyed each plot for gopher disturbance. Here we are only presenting data for the 2018/2019 season. The data consisted of random, independent samples that were normally distributed, so parametric models were used for analysis. Specifically, an Analysis of Variance (ANOVA) was used to compare the growth and reproduction of purple needlegrass in the three watering treatments during the 2018/2019 growing season followed by a Tukey HSD (honestly significant difference) means separation test. An ANOVA and Tukey HSD were also used to compare the amount of gopher disturbance in each of the watering treatments. Since gopher activity was not manipulated we were unable to compare the independent effects of watering treatment and gopher activity. However, we used multiple linear regression to investigate the relationship between gopher damage and the basal circumference and reproductive output of purple needlegrass while accounting for the effect of watering treatment as a covariate.

Results

We found that gopher activity negatively impacted purple needlegrass regardless of watering treatment (Figure 1). As gopher damaged increased, both average basal circumference ($F=19.61$, $R^2=0.2941$, $p<0.0001$; Figure 1A) and reproductive output ($F=6.867$, $R^2=0.1226$, $p<0.0001$; Figure 1B) declined.

There was also a significant impact of watering treatment on the basal circumference ($F=11.79$, $p<0.0001$; Figure 2A) and reproductive effort ($F=5.203$, $p=0.007$; Figure 2B) of purple needlegrass. Individuals in the droughted treatment were significantly smaller than individuals in the ambient ($p=0.001$) and water addition treatments ($p<0.0001$) with no difference between ambient and water addition plants ($p=0.47$). Reproductive output, on the other hand, was greatest in the water addition treatment, compared to drought ($p=0.02$) and ambient ($p=0.02$), with no difference in reproductive output between ambient and water addition plants ($p=0.95$).

Finally, we also found that gopher damage differed significantly between the three watering treatments ($F= 12.72$, $p=0.00108$; Figure 3), with the drought treatment having significantly more damage than the ambient and water addition treatments ($p=0.001$ and $p=0.008$ respectively). There was no significant difference in gopher damage between the ambient and water addition treatments ($p=0.512$).

Discussion

We found that valley pocket gophers have a significant negative impact on the growth and reproduction of purple needlegrass (Figure 1), especially when water is reduced (Figure 3). This suggests that gopher activity could potentially be a larger problem for restoration during dry years due to the additional stress on the plants. Since gopher activity was higher in the drought plots, and we had no drought treatments without gopher activity, it is not possible to tease apart the independent effects of drought and gophers with this experiment. However, our results suggest that gopher activity is likely to have a particularly negative impact on reproductive success as drought alone did not decrease reproduction (Figure 2) but increasing gopher activity did (Figure 1B). While our experiment was not able to separate the effect of drought and gophers on reproduction, previous research has also found that drought does not reduce reproduction output. For example, Fitch *et al.* (2019) found that while increasing water led to greater culm production, plants in the lowest watering treatment produced the same number of culms as those in the control treatment. Therefore, we believe that the decrease in reproductive output was either directly due to increased gopher activity or due to a synergetic effect between gophers and drought. Our results highlight the importance of incorporating animals into restoration planning,

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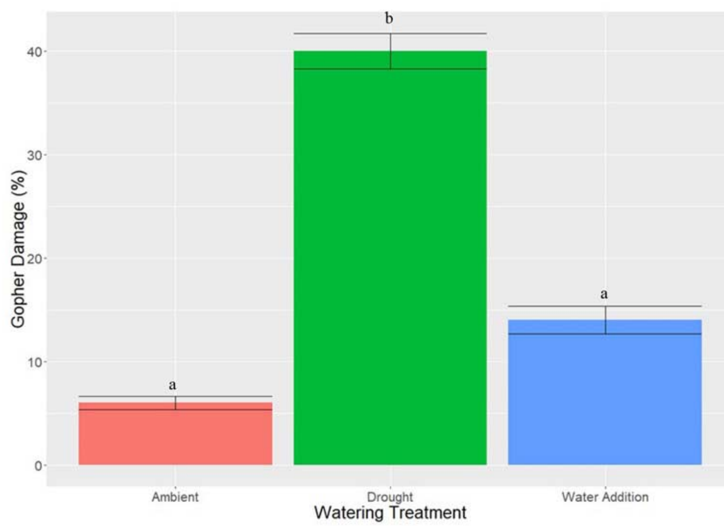

Figure 3. The average gopher damage within each watering treatment. The ambient treatment was the control, the drought treatment received a 50% reduction in precipitation, and the water addition treatment received an additional 4 weeks of water at the end of the growing season. Error bars indicate ± SE with letters indicating significant differences as measured by an Analysis of Variance.

especially when considering how climate change will impact future restoration success.

With droughts expected to become more common in California grasslands in the future (AghaKouchak *et al.* 2014), it is important to understand what factors are going to impact the survival of native species that are commonly targeted for restoration. Knowing how to approach restoration efforts during drought years is critical for practitioners to adjust restoration plans to maximize the likelihood of plant establishment and survival. Understanding impacts on perennial bunchgrasses, like purple needlegrass, is particularly important as these species are often the primary focus in restoration efforts (Stromberg *et al.* 2007). Our results suggest that gophers are likely to amplify the negative effect of gophers on native perennial grasses (Stromberg and Griffin 1996, Watts 2010) during dry years and should be considered when starting or maintaining grassland restoration sites during a drought.

Traditionally, restoration efforts tend to disregard the potential negative impacts of wildlife, focusing more on floral community success (Keesing and Wratten 1998). Ignoring the effects of animals, however, could lead to declines in plant survival and ultimately to restoration failure. We are not advocating for the removal of native animals from grassland restoration sites, as these species are an integral part of the community and native to these ecosystems. For example, valley pocket gophers provide valuable ecosystem services such as nutrient cycling, and promoting native species that rely on disturbance for dispersal (Reichman and Seabloom 2002). Thus, attempts to remove gophers from the system could negatively impact the ecosystem as a whole despite benefiting purple needlegrass. However, our results do suggest that during a drought, gopher activity could be minimized by caging sensitive plants or watering seedlings to reduce the increase in damage during already stressful dry years. As frequent and prolonged droughts increase throughout California in the coming decades, practitioners need to adapt and change management plans during dry years to account for their unique challenges. Also, as we move forward with restoration ecology, animals and animal behavior need to be further integrated into restoration planning to successfully restore native ecosystems (Halle *et al.* 2004, Lindell 2008). Only when we start thinking about the relationships between native animals and plants, and how to facilitate positive interactions between these species, will we be able to successfully restore resilient, self-sustaining communities in the future.

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