**The Impacts of Drought and Competition with Invasive Red Brome (*Bromus madritensis* subspecies *rubens*)** **on Californian Native Plant Communities**

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**Abstract**

Native Californian plant communities are under serious threat due to increased severity and frequency of drought, combined with the progressive expansion of invasive plant species. Red brome is currently one of the most rapidly spreading invasive plants in California and with a suite of competitive advantages, it is driving rapid declines in native plant diversity. The present study explores the combined effects of drought and an invasive competitor (red brome) on three native Californian plants. The experiment was performed in a controlled greenhouse setting in order to reduce the impact of extraneous variables on the results of the study. It was observed that red brome had no effect on native mortality but significantly reduced native productivity. Drought increased native mortality and decreased native productivity. Furthermore, red brome mortality and biomass per individuals was most negatively effected when grown with Phacelia with drought significantly increasing brome mortality. The negative effect of brome on native productivity implies decreased fecundity for native populations forced to compete with brome. However, Phacelia was observed to be the most resilient plant to brome as well as the best suppressor of brome and should therefore be considered as a competitor species for future brome restoration programs.

**Introduction**

California is known for having an extremely unique plant ecology, with a vast array of very different microclimates and biomes. The southern portion of the state is defined by an arid precipitation regime and as a result is dominated by chaparral and desert ecosystems. The chaparral environments possess a mediterranean climate; hot, dry summers and mild, wet winters (Zammit and Zedler, 1994). The deserts, which are located in the southeastern most portion of the state and extend into Arizona and Nevada, possess a climatic regime of hot, dry summers and cold, dry winters (Thomson et al., 2018; Larrain-Barrios et al., 2018).

In both chaparral and desert ecosystems, water availability tends to be the greatest environmental filter in determining which plant species persist (Larrain-Barrios et al., 2018). In order to survive under these stressful conditions, plants must possess a suite of unique functional traits. Small, thick waxy leaves or the adaptation of spines (which are modified leaves) helps to reduce water loss from evapotranspiration (Larrain-Barrios et al., 2018). A deep, rapidly growing, tap-root system aids in both water absorption from deeper areas of the soil profile and the storage of vital nutrients (Barbour, 1973). The production of small seeds, with a thick seed coat, prevents desiccation during periods of dormancy, due to undesirable growing conditions (Keeley, 1991). Sets of hairs or trichomes along leaves and stems aid, in foliar uptake of moisture from fog and morning dew, in tandem with increasing reflectance of surfaces, thereby reducing damage from high-irradiance (Larrain-Barrios et al., 2018). Finally, presence of green stems (photosynthetic tissue) aids in carbon sequestration during leafless periods and severe drought (Larrain-Barrios et al., 2018). Plants that lack these traits are unable to survive the resource limited and arid environments of Southern California.

California is also estimated to possess 6000 native plant species of which 2200 are endemic; they are found nowhere else on Earth (Myers et al., 2000; Loarie et al., 2008). Brooks et al., (2006) defines California as a centre of plant biodiversity containing a high degree of irreplaceability. Furthermore, the state is home to approximately 71 endemic vertebrate species combined with an exceptional amount of arthropod biodiversity, many of which are endemic to California (Myers et al., 2000; Prugh et al., 2018). All of these animal species rely on the persistence of the native floristic communities in order to thrive. Due to the high degree of endemism found in California, it is considered one of the world’s biodiversity hotspots (Myers et al., 2000). A biodiversity hotspot is defined as a region under threat due to ecological or anthropogenic factors and contains a significant amount of the world’s endemic plant and animals species (Brooks et al., 2006; Myers et al., 2000). In regards to California, native plant communities, particularly in the chaparral and desert ecosystems, are currently under significant threat due to two major ecological factors; 1) increased frequency and severity of drought and 2) ecological invasion of exotic plant species.

**The Californian Drought**

Southern California is defined by an arid (desert) or semi-arid (chaparral) climatic regime where precipitation is the primary environmental factor that determines the success and proliferation of vegetative communities. Because of the extreme impact that water availability has on these ecosystems, rapid ecological changes occur in response to varying precipitation levels, both seasonally and over a multi-year period (Swain et al., 2018). In Southern California, the growing season coincides with the winter rains, which typically begin in late October and end in April (Thompson et al., 2018). In May, the summer drought begins with herbaceous annuals dispersing their seeds and dying shortly after; only cacti and and deeply rooted, sclerophylls (possess small, thick, waxy leaves) shrubs persist until the winter rains return (Wade and Loik, 2017). This is a typical depiction of the seasonal ecological changes which occur in Southern California plant communities.

From 2012 to 2016, California underwent a severe multi-year drought. Although drought periods are characteristic of the climate of Western North America, the 5-year California drought was not only the worst drought in over a century of instrumental observation but the most severe drought in the last 1200 years (Griffin and Anchukaitis, 2014). The severity of the drought was prescribed to multiple years of below average precipitation and above average temperatures, with 2014 being the driest out of the 5 years (Swain et al., 2016). The higher temperatures accounted for approximately 25% of the observed moisture deficits, reducing soil moisture, streamflow/discharge and water levels in human-made water storage reservoirs. In turn, the drought imposed both negative societal and ecological impacts (Lund et al., 2018).

From a societal perspective, the drought caused drastic economic losses for California’s agricultural industry. In 2015 alone, there was a $900 million loss in crop revenues and an extra $590 million rise in irrigation costs; when culminated with other factors, the total loss for the year was $2.7 billion (Lund et al., 2018). Furthermore, isolated and rural cities in Southern California had to perform mandatory water rationing in order to cope with rapidly depleting water supplies (Lund et al., 2018).

Nevertheless, the majority of concern regarding the California drought has been in terms of the ecological effects. The drought tolerant plant species of Southern California typically employ one of three mechanisms in order to survive extended and sever drought periods; tolerance, avoidance and escape (Balachowski et al., 2018). Tolerance is utilized by plants that can withstand significant levels of tissue dehydration in the absence of additional water inputs. They survive by storing large quantities of water-soluble proteins and carbohydrates, which aid in regulating osmotic potential and provide nutrient reserves for regrowth once the water stress in alleviated (Volaire, 1995). Avoidance is utilized by plants that are relatively sensitive to dehydration and try to delay dehydration for as long as possible. This is achieved through the use of a deep root system capable of tapping into groundwater reserves (Balachowski et al., 2018; Young et al., 2010). Both tolerance and avoidance are utilized by perennials (live longer than a single growing season) in an attempt to survive the summer drought. Escape is characteristic of plant taxa that grow rapidly, reproduce and die before ever having to experience severe drought stress. This is observed in annual plants inhabiting Southern California ecosystems (Balachowski et al., 2018). In a severe drought however, plants that utilize avoidance and escape strategies are at significant risk. As observed in the California drought, groundwater reserves gradually deplete due to high temperatures and low hydrological inputs (Lund et al., 2018). This puts high stress on plants that perform the avoidance strategy as the groundwater flow is their primary ‘life-line’ to survive the drought (Young et al., 2010). Plants that perform the escape strategy require sufficient winter rain in order to grow and reach reproductive maturity. If this threshold of rain is not reached, the plants will die before reproducing resulting in significant decreases in population size and genetic diversity (Thomson et al., 2018). Even if reproductive maturity is achieved by an annual plant, due to the lack of resources, lower fecundity (reproductive output) occurs resulting in reduced seed quality and in turn reduced germination success in the following growing season (Thomson et al., 2018).

Drought tolerant plants are also capable of performing seed dormancy; once dispersed, the seeds will remain in the soil and only germinate once sufficient levels of rainfall (gauged by soil moisture content) are detected (Keeley, 1991). This is a very successful strategy for evading unfavourable growing conditions, however over successive dry years, the viability of the seeds decreases, reducing the number of germinating seedlings once the drought is over (Harrison et al., 2015). This strategy is also susceptible to the timing of rain events. If a very large rain event occurs in the early winter months, but the successive months are plagued by low precipitation, only a minority of the germinated seedlings will survive to adulthood due to intense competition in the presence of extremely limited resources (Levine et al., 2011).

With impending anthropogenic driven climate change, the frequency and severity of droughts is expected to increase in future years. It is predicted that over the next 80 years average precipitation in Southern California will decrease by a maximum of 10%, combined with a 1-3 degree Celsius increase in average temperatures (IPCC AR5, 2014). Novel restoration tactics therefore must be explored in order to mitigate future ecological damage to plant communities of Southern California.

**The Californian Invasion**

The spread of exotic plant species has rapidly increased over the course of the last few centuries, primarily due to the rapid geographic expansion of human populations (Salo, 2005). The dispersal of these species has been both intentional (for ornamental purposes) and accidental (propagules being unknowingly transported from one location to the next). An exotic species is simply defined as a non-native species (Pysek et al., 2017). In some cases, these exotic species become established (also known as naturalized) and impose no threats to the native community. However, if the exotic species is observed to impose negative impacts on the native environment, then it is deemed an invasive species (Pysek et al., 2017). Invasive plant species have been observed to cause rapid shifts in the ecological composition of the native ecosystems in which they invade. California contains 1753 naturalized exotic plant species; the greatest number of any region in the world (Pysek et al., 2017). Of those naturalized exotic plant species, an estimated 209 are invasive (Pysek et al., 2017). The majority of the invasive plant species of California originated from Eurasia and Northern Africa; 71% (Rejmanek and Randall, 1994). The invasive species which originated from Eurasia and Northern Africa are also the most successful invasive plant species in California due to the similar climatic regime of the Mediterranean; the invading plants are not forced to overcome a significant climatic barrier (Rejmanek and Randall, 1994). Although, the rate of introduction of exotic plant species has dramatically declined over recent decades, the geographical ranges of established invasive plant species have been rapidly expanding since their introduction into California (Rejmanek and Randall, 1994). This rapid expansion has crowded out native plant populations, leaving many ecosystems, particularly in Southern coastal California, with low native species richness (Salo, 2005).

Red brome (*Bromus madritensis* subspecies *rubens*), is a winter annual grass part of the Poaceae family, with an average height of 20cm to 70cm, native to the Mediterranean. It has rapidly invaded both disturbed and undisturbed habitats in the Mojave Desert, San Joaquin Valley and chaparral environments along the coastline of Southern California (Salo, 2005). Red brome is highly competitive and has been observed to extirpate both native annual and perennial plants in southern Californian ecosystems (Salo, 2005). This competitive advantage arises from a suite of botanical traits. Firstly, red brome extracts soil moisture at a much faster rate than native plants, allowing it to germinate before the native plant community once the winter rains begin (DeFalco et al., 2003). Secondly, red brome is capable of extracting greater quantities of soil nitrogen than the native plants. This allows red brome to invest greater amounts of nutrients into biomass production and in turn, crowd out neighbouring competitors (DeFalco et al., 2003). Finally, red brome invests a large amount of energy in the growth of an extensive root system. This explains its high affinity for resource acquisition. This extensive root system also acts as a storage for nutrients (DeFalco et al., 2003). Therefore, if eaten by a predator or cut manually (as attempted in many biocontrol tactics) the red brome can rapidly regenerate utilizing the nutrients it has stored in its roots (DeFalco et al., 2003; Salo, 2005). The competitive advantages which red brome possesses has been linked to decreased growth and fecundity of native annual plants (Inouye et al., 1980).

Furthermore, at the end of the growing season the dead brome biomass acts as fire fuel, increasing the rate of fires in invaded habitats. These fires kill native fire-intolerant plants, such as succulents and woody shrubs, while also decreasing the viability of native seeds laying dormant in the soil (Salo, 2005). Essentially, through the use of fire, red brome clears the landscape, allowing it to dominate the plant community. Due to the imposing threat of Brome on native Californian ecosystems, it is an exemplary invasive species for analysis.

**Previous Research and the Present Study**

The effects of drought and red brome has been analyzed previously under natural conditions. Thomson et al., (2018), observed that both drought and competition with brome altered the survival and productivity of two native species common to California semi-arid grasslands. Drought increased both native mortality and brome mortality. In wetter years brome and native germination increased relative to dry years however, over the course of the growing season native plant abundances rapidly declined. Those native plants that did survive to the end of the growing season possessed greatly reduced shoot length, flower size and seed production compared to control plants grown in the absence of brome. The negative impacts of drought and invasive plant species was further examined by Pinto and Ortega (2016), who found that invasive plants significantly increase their cover in experimental plots that are exposed to regular severe droughts when compared to plots that were not exposed to such disturbances. Furthermore, in drought plots, invasive plant cover was unaffected by native species richness. Restoration tactics for controlling the spread of invasive species must be proactive rather than reactive, as highly diverse native species assemblages appear to have no effect in invaded ecosystems where invasive plant density greatly exceeds native plant densities (Pinto and Ortega, 2016).

A study performed by Mason et al., (2016) was consistent with the previously discussed experiments as it was observed that competition with an invasive plant always reduced the success of native plant populations when compared to natives that were grown in the absence of the invasive species. However, the effect of water availability was species specific; some natives performed better under dry conditions whereas others performed better under wet conditions. This study displayed that the negative effects of competition with an exotic species is not always exacerbated under drought like conditions. Further research must be performed in order to specifically determine how red brome effects native populations and how native Californian plants respond to this competition across varying water availability.

In order to determine the response of native Californian plant communities to drought and ecological invasion, the present study analyzes the productivity and survival of three plant species native to chaparral and desert habitats in Southern California to the presence and absence of red brome across watering regimes ranging from extreme drought to extremely wet. *Plantago insularis* (Plantago), *Salvia columbariae* (Salvia), and *Phacelia tancetifolia* (Phacelia) were selected as the native species. This is due to their resilience and prominence in a vast array of southern California microclimates, thereby allowing them to be utilized as phytometers. A phytometer is an indicator plant species that provides information on the conditions and quality of an ecosystem through analysis of traits such as plant survival, germination, growth and reproductive output (Strobl et al., 2018). Phytometers are commonly utilized in ecosystem restoration strategies as a method of determining how the ecosystem is damaged or how changes to the ecosystem can be expected to alter the quality of the plant community (Strobl et al., 2018).

Many of the studies analyzing the effects of drought or invasive species have been performed in an uncontrolled ecological setting. Although, these large scale experiments produce results which are expected to be observed under natural conditions, there are many extraneous variables at work which can alter the growth characteristics of the plant community being analyzed (Thomson et al., 2016; Ignace et al., 2018). The present study therefore utilized a controlled greenhouse setting in order to focus on the effects of an invasive species (red brome) and watering availability on the growth and survival of the three phytometer species. It is hypothesized that availability of water, the presence of an invasive species, and the interaction between these two variables will determine the productivity and survivorship of the three native Californian plants examined in the present study. It is also hypothesized that brome mortality and productivity will be dependent on water treatment and the native species with which it is competing. It is predicted that 1) all three native plants will have the highest mortality and lowest individual biomass when grown with brome under drought conditions; 2) the growth and survival of native plants will be greater without brome, across all water treatments; 3) brome will experience high mortality and low productivity under drought conditions; 4) Phacelia will be the best suppressor of brome and possess the lowest mortality and greatest productivity. By utilizing an array of three phytometer species, the present study aims to determine not only how plant invasion and drought will alter Californian plant communities, but also what conditions and plant communities must be utilized in order to restore damaged ecosystems and reduce the negative effects imposed by these two impending threats.

**Methodology**

**Study Species**

*Plantago insularis* (Plantago) is an annual grass belonging to the Plantiginaceae family, growing to a maximum height under 1 ft and producing small white flowers, 3mm to 5mm in diameter. It is commonly found in semi-arid grasslands and desert environments. It possesses an intermediate water use efficiency and relative growth rate making it an ideal species for short term, drought-tolerance experiments (Gremer et al., 2013). Plantago is highly sensitive to precipitation events (rapidly increases productivity and growth), has a low respiratory carbon loss and the ability to rapidly alter physiological processes based on environmental temperatures (Barron-Gafford et al., 2013). Plantago is also a graminoid (herbaceous plant with a grass-like morphology), making it unique as the other two native species analyzed in the present study are forbs (a herbaceous flowering plant that is not a species of grass).

*Salvia columbariae* (Salvia) is an annual forb belonging to the Lamiaceae family, growing to a height between 10cm and 50cm and producing pale blue flowers. Salvia is most prominent in coastal sage scrub and chaparral habitats with well-drained soils (Funk and Zachary, 2010). It is tolerant to drought due to its thick waxy leaves (reduces evapotranspiration) and ability to perform foliar uptake of fog in overnight and early morning periods (Emery, 2016). These traits tend to be associated with a high water use efficiency. However, Salvia does require open areas, with an abundance of sunlight in order to maximize productivity(Emery, 2016). Nevertheless, Salvia is utilized in seeding and restoration programs on abandoned agricultural land due to its ecological resilience (Marushia and Allen, 2011).

*Phacelia tancetifolia* (Phacelia) is an annual forb belonging to the Boraginaceae family that can grow to a maximum height of 100cm and producing clustered, bell-shaped purple flowers. Phacelia is widespread throughout grassland and desert habitats of the Southwestern USA (Kilian, 2016). It is drought tolerant with a high water use efficiency and a high relative growth rate. Due to its high growth rate (and therefore high biomass production) and tendency to attract and sustain pollinator populations, Phacelia is commonly used as a cover crop plant (Kilian, 2016). Although considered a very resilient species, light availability tends to be a determining factor in germination; if seeds are buried too deep or neighbouring plants block out sunlight, phacelia germination success is substantially reduced (Kilian, 2016).

**Experimental Procedure**

The experiment was a three level, fully randomized, factorial design. There were three native treatments (Plantago, Salvia, and Phacelia) each with 100, 5cm radius pots and therefore 300 pots total. There were two brome treatments within each of the native treatments; a brome present and a brome absent treatment with 50 pots for each treatment, of the 100 dedicated to each native treatment. Across each grouping of 50 pots (ie. plantago with brome (50 pots) and plantago without brome (50 pots)), 5 watering regimes were tested with each watering regime having 10 replicates. The watering regimes utilized in the present study were 80mm, 150mm, 200mm, 250mm, and 330mm of rain. These watering regimes range from an extreme drought to and extremely wet year based on precipitation data collected from the San Joaquin Valley, California. In the No Brome treatments a total of 10 native seeds were planted in every pot, while in the Brome treatments 10 native seeds and 10 brome seeds were planted in each pot. Plants were grown in a a soil mixture consisting of: 2/3 of a bag of Alltreat Farms Sand, 1/2 bag of Alltreat Composted Sheep Manure, 1 bag of Alltreat 3-Way Mix Garden Soil and 1 bag of Berger All-Purpose Mix Potting Soil. All pots were randomly assigned a treatment and subsequently seeded. Using a sieve, the seeds were lightly covered with additional soil in order to simulate the build up of biomass and debris which occurs over the dry season. A greenhouse light, with a 12 hour on - 12 hour off schedule was placed over the plants to ensure they received light levels equal to that experienced during the California growing season. Seeds were sown on September 27th 2018 and the first watering period was performed on October 1st 2018. The pots were left to grow for a total of 10 weeks; the experiment concluded on December 6th 2018.

In order to simulate natural rain events and intermittent periods of dry weather, all pots were watered once every ten days. Therefore, over the course of the 10 week period, 6 watering periods were performed. Each watering period, pots were given a fixed volume of water pertaining to their designated watering regime. The precipitation measurements obtained were based on a standard 2cm radius weather gauge (National Weather Service) and therefore had to be converted to the proportional water volume which would be expected to fall on a 78.54cm^2 circle of ground (based on the 5cm radius pots utilized in the present study). This calculation was performed using a simple ratio between the volume of the weather gauge and the volume of the 5cm radius pots. Once the total volume of water was determined for each precipitation regime, it was divided by 6 (the number of watering periods) to determine the amount of water provided to each pot, at each watering period.

**Data Collection**

Three census were performed throughout the experimental period; a germination census (performed on October 12 2018, 2 weeks into the experimental period), an establishment census (performed on November 2nd 2018, 5 weeks into the experimental period), and a final census (performed on December 6th 2018, at the conclusion of the experiment). At each census, the number of plants per species in each pot was counted. This census data was converted to proportional survival (at each census) based on the fixed number of seeds per species (10 seeds) planted in each pot. After the conclusion of the experiment, four productivity measurements were taken for each pot; total aboveground biomass per species, percent soil moisture, mortality rate per species, and average biomass per individual.

All aboveground biomass in each pot was clipped and separated based on species and treatment. All samples were placed in paper lunch bags and dried in a Yamato DKN900 Mechanical Convection Oven at 65 degrees Celsius for a 48 hour period. All samples were then weighed using an electronic scale accurate to 4 decimal places.

Soil moisture measurements were taken after all biomass had been removed from the pots in order to ensure minimal disturbance and damage to the plants. In order to ensure the pots were accurately acclimated to each of the watering regimes, a seventh watering period was performed after all of the aboveground biomass had been clipped. The pots were left for a 24 hour period after this seventh watering period in order to ensure the equilibration of the soil moisture. Soil moisture measurements were performed using a Delta Technologies AT Soil Moisture Kit.

Mortality rate per species per pot was calculated using the equation [1 - Proportional Survivorship at Census Three]. This calculation defines mortality as all individuals which did not germinate or germinated but did not survive to the conclusion of the experiment. Average biomass per individual per pot was calculated using the equation [Total specific biomass per pot/Number of Individuals per Species at Census Three]. This measurement allowed for the determination of the average productivity investment per individual per species across all 300 replicates.

**Data Analysis**

General linear models (GLM) were utilized to determine how both native and brome mortality and biomass per individual differed across water treatments. In tandem with the GLMs, post-hoc Tukey tests were performed in order to determine which water treatments were significantly different from one another. Independant sample t-tests were also performed to determine if native mortality and productivity was significantly different with and without brome across each of the five water treatments. One-way ANOVAs were performed to determine how native mortality and productivity differed across the different native species as well as how brome mortality and productivity differed when grown with the different native species. Finally, four global GLMs were performed to analyze if there was significant interaction between the independent variables (Native Species, Water Treatment, and Brome Treatment) in determining native and brome mortality and productivity. All statistical procedures were performed in IBM’s SPSS.

**Results**

**1) Soil Moisture**

The water treatments followed a stepwise pattern of increasing soil moisture [Figure 1]. The 80mm and 150mm treatments were significantly different from all other water treatments, and therefore accurately simulated the watering regime of a drought. The 200mm treatments was different from all other watering regimes and simulated an average Californian watering regime. The 250mm and 330mm treatments were significantly different from all other water treatments and depicted an above-average rainy season. All differences were supported by P<0.001.

**2) Germination**

The germination rates of the three native species were significantly different from one another, across all treatments (P<0.001) [Figure 2]. Plantago had the greatest germination rates across all treatments, while Salvia possessed the lowest germination rates across all treatments. Increased water availability appeared to increase germination however the trend was not significant [Figure 2]. Furthermore, the presence or absence of brome also did not have a significant effect on native germination. Brome germination did not vary significantly when grown with the different native species or across water availability [Figure 5A].

**3) Native Mortality**

It was observed that native species (df = 2, P<0.001) and water treatment (df = 4, P<0.001) had a significant effect on native mortality, however the presence or absence of brome did not have a significant affect on native mortality [Table 1A]. Furthermore, the global model of water treatment by native species by brome treatment was not a significant model. When only native species by water treatment was analyzed, there was still no significance of the model [Table 1A]. The combined three variable model possessed an R^2 of 0.845. Across all water treatments and both with and without brome, Plantago possessed the lowest mortality while Salvia possessed the greatest mortality, with greater than 75% in all treatments [Figure 3]. Native mortality for all three species was not significantly different when grown with and without brome. Plantago and Phacelia experienced significantly higher mortality rates under drought conditions (80mm and 150mm) when compared to the 330mm treatment (Plantago: P = 0.037, Phacelia = 0.036). For Salvia, there was no significant trend in mortality across increasing water availability [Figure 3].

**4)** **Native Biomass/Individual**

When analyzed individually, all three independent variables had a significant effect on native biomass/individual (P<0.001 for each variable), with native species possessing the greatest effect size out of the three variables [Table 2A]. Furthermore, the global model (interaction between Native Species by Water Treatment by Brome Treatment) displayed there was significant interaction between the three variables in determining native biomass/individual (P = 0.032); this model possessed an R^2 = 0.505 [Table 2A]. Averaged across all of the water treatments, Phacelia possessed the greatest biomass/individual while Salvia possessed the lowest biomass/individual [Figure 4]. For all native plants, the 330mm treatment always produced greater biomass/individual than the 80mm treatment, however there was not a smooth increasing trend of biomass/individual across increasing water availability [Figure 4]. Phacelia biomass/individual was only significantly greater between the brome and no brome treatments at the 330mm treatment (P = 0.007). Plantago had significantly lower biomass/individual at the 80mm, 150mm and 200mm treatments when grown with brome (80mm: P = 0.007; 150mm: P = 0.016; 200mm: P = 0.16). Salvia has significantly lower biomass/individual with brome at the 80mm treatment (80mm: P = 0.006).

**5) Brome Mortality**

Water treatment (P<0.001) and native species (P<0.001) were both significant in determining brome mortality [Table 1B]. Furthermore, the model of native species by water treatment was not significant in determining brome mortality (R^2 = 0.338). Across all water treatments, brome possessed the greatest mortality when grown with Phacelia, and the lowest mortality when grown with Salvia (P<0.001) [Figure 5B]. Brome mortality was significantly higher at the 80mm water treatment across all three native species (Plantago: P = 0.005; Phacelia: P = 0.001; Salvia: P = 0.006) [Figure 5B].

**6) Brome Biomass/Individual**

Native species was the only variable that had a significant effect on brome biomass/individual (P<0.001);the effects of water treatment were not significant [Table 2B]. Furthermore, the combined model of native species by water treatment was also not significant in determining brome biomass/individual (R^2=0.256) [Table 2B]. Brome biomass/individual was greatest with Salvia, across all water treatments and lowest when grown with Phacelia, across all water treatments (P<0.001) [Figure 5C]. However, within each native species treatment, brome biomass/individual did not differ significantly across the water treatments. When grown with Salvia, increased water availability tended to increase brome biomass/individual, whereas when grown with Plantago and Phacelia, increasing water availability decreased brome biomass/individual [Figure 5C]. However, none of these trends were significant.

**Discussion**

The present study successfully analyzed the effect of brome and water availability on the productivity and survivorship of three native California annuals. However, the hypothesis was only partially supported as brome treatment and water availability did not ubiquitously explain variation in native mortality and productivity. The particular native species being analyzed had more significance in determining mortality and productivity; an unexpected finding. Furthermore, brome mortality and productivity was significantly related to the native species with which the brome was competing. Water availability, which was expected to play a defining role in brome success, only affected brome mortality and had no influence on brome productivity.

Native mortality was significantly affected by water availability and native species, while brome treatment had no effect on native mortality. The global model, which analyzed interactions between the three independent variables was not significant, displaying that water availability and brome treatment affected each native species similarly. Native species was the greatest independent factor in determining mortality as it possessed the greatest effect size out of all the independent variables. Furthermore, native species was the the only significant variable in determining native germination. Plantago, possessed the greatest germination and lowest mortality across all treatments, going against the predictions of the present study. Environmental cues and conditions for germination are vital in order to understand the survivorship of a plant population as the germination stage is the most vulnerable stage in the life of an annual plant (Clauss and Venable, 2000). Plantago germination, like most desert annuals, is induced by precipitation. Plantago however, has a unique ability to exhibit phenotypic plasticity at the germination stage, solely in response to water availability (Clauss and Venable, 2000). Clauss and Venable (2000) observed Plantago germination in 12 different populations with each population possessing a unique precipitation regime. Increasing water availability increased germination rates however, the Plantago appeared to perform rapid microevolutionary changes in response to water availability in order to maximize germination under resource limiting conditions (Clauss and Venable, 2000). Plantago has also been observed to possess a wide range of germination dates; it is capable of germinating later in the growing season given specific environmental conditions; abundance of rainfall occurring in tandem with an cool temperatures (Clauss and Venable, 2000; Barron-Gafford et al., 2013). This ability to perform late-season germination may have induced Plantago’s lower mortality rate as new individuals could have sprouted throughout the experimental period; a trait not observed for either Phacelia or Salvia (Emery, 2016; Kilian, 2016). However, due to the ability of Plantago to alter its germination characteristics based on water content, as well as its ability to delay seed dormancy, the high germination rates and low mortality rates observed for Plantago are consistent with its life history traits.

Phacelia and Plantago experienced decreasing mortality across increasing water availability. This relationship is well documented in desert ecosystems as the abundance of a generally limited resource drives greater rates of germination and subsequent survival throughout the growing season (Copeland et al., 2016; Balachowski et al., 2018). Salvia possessed no significant trend in mortality across increasing soil moisture. Mortality rates were also consistently high, exceeding 75% in all treatments. The abnormally high mortality rates observed for Salvia contrast with those observed in previous studies. Salvia is commonly used in the ecological restoration of disturbed or invaded ecosystems due to its high competitive ability and resilience to a wide array of temperatures and precipitation regimes (Marushia and Allen, 2011). Furthermore, the Salvia seed density used in the present study did not exceed those utilized in restoration programs, therefore intraspecific competition between Salvia individuals was not the cause for the reduced germination and high mortality rates (Toth and Huse, 2014). Poor seed quality is theorized to have been the cause for high Salvia mortality.

The mortality of all three native species did not differ when grown with and without brome. This was an unexpected observation. When competing with only grass species, brome is observed to reduce native grass cover from 73% to 99% (Young et al., 2014). Brome has also been observed to reduce the survival of forbs by up to 75% invaded habitats (Thomson et al., 2016). This increased native mortality of native annual populations is attributed to the rapid germination and growth of red brome, allowing the brome to crowd out native plants reducing the light levels that reach the soil surface thereby suppressing native germination (Salo, 2004).However, Salo et al., (2005) observed similar results as the present study with emergence and survival of native species being insignificantly affected by the presence of red brome. It is theorized that the phenotypic plasticity associated with desert annuals allows them to germinate and survive adequately even in the presence of an invasive competitor (Salo et al., 2005). Furthermore in natural invaded sites, red brome seed density is much greater than native seed density (Salo et al., 2005), however the present study utilized equal seed densities; ten brome seed and ten native seeds. These equal seeding densities may have prevented the excessive crowding out effect which brome relies upon in order to suppress the germination of native species thereby causing insignificant differences between brome and no brome treatments.

Native biomass per individual was significantly affected by native species, water availability and brome treatment, independently. Native species was the most significant predictor of native biomass per individual as it possessed the greatest effect size. Phacelia possessed the greatest biomass across all treatments, supporting the predictions of the present study. Firstly, under natural conditions, Phacelia is on average the largest of the three native species thereby giving it an advantage for biomass measurements (Killian, 2016). Furthermore, Phacelia is known for its rapid growth and high investment in aboveground biomass (Killian, 2016; Turson et al., 2018). These traits of rapid growth and high aboveground productivity are intertwined. Phacelia invests large quantities of energy into aboveground biomass in order to maximize leaf surface area in turn maximizing growth and photosynthetic output (Fuksa et al., 2013). Furthermore, the cells which compose the stem and nodes of the Phacelia plant are also capable of high levels of photosynthetic activity (Larrain-Barrios et al., 2018). This ensures that in times of extreme resource limitation when large number of leaves can no longer be produced and maintained, Phacelia can maintain sufficient levels of photosynthesis though utilizing the photosynthetic capabilities of its nodes and stems (Fuksa et al., 2013; Larrain-Barrios et al., 2018).

Water availability was the second most significant variable in determining native biomass per individual, with greater water availability in turn driving greater biomass per individual. This is a well documented observation in desert ecosystems. Under stressful conditions where water is extremely limited, desert plants invest the majority of their primary production into below ground biomass in an effort to expand their root system and in turn maximize water absorption (Barbour, 1973). However, once water is no longer a limited resource, desert plants alter where they invest their productivity and subsequently increase their investment in aboveground biomass in an effort to increase photosynthetic surface area and height (Burri et al., 2018). This leads to the plant possessing a greater growth rate, increases competitive ability, increases fecundity through the production of larger flowers that are more noticeable to pollinators, and increases seed size (Eckstein, 2005).

Brome treatment was the lowest predictor of native biomass per individual, nevertheless every native species experienced significantly lower productivity when grown in the presence of brome, thereby supporting the predictions of the present study. Salo et al., (2005) observed similar results with red brome reducing native biomass per individual by 72 to 89%. This reduction in biomass was linked to reduced plant height and fecundity at the conclusion of the growing season. The negative impact of red brome on native biomass per individual is a serious threat to the long term persistence of native annual plant populations (Salo et al., 2005). This is because as the native plants germinate, they are faced with extreme competition due to the neighbouring red brome. Intense competition in a resource limited environment, reduces the size and fecundity of the native plants and subsequently induces reduced seed production (Salo et al., 2005). The vast majority of native desert annuals rely on soil seed reserves to proliferate and maintain a healthy population (Keeley, 1991). Therefore, over multiple years of reduced fecundity and seed production, the soil seed reserves of annual desert plants begin to deplete thereby threatening their continued existence in ecosystems invaded by red brome (Salo et al., 2005). Furthermore, the global model for native biomass per individual was significant; there were significant interactions between native species, brome treatment and water treatment. This finding implies that the effects of water treatment and brome treatment are species specific; a finding previously observed by Mason et al., (2016). Therefore, strategies for the biocontrol of red brome populations must be first analyzed at the species level in order to determine which native species are the most resilient to red brome invasion and under what abiotic conditions does this resilience peak.

Brome germination was not significantly different across the native species or across water treatments however, both variables had a significant effect on brome mortality. Water treatment was the stronger determinant of brome mortality with drought conditions driving significantly greater brome mortality, thereby supporting the predictions of the present study. Red brome is a relatively drought intolerant mediterranean annual due to the fact that it possesses a low water use efficiency (Nguyen et al., 2016; DeFalco et al., 2003). Red brome is also extremely sensitive to precipitation events; even the slightest rainfall will cue the brome to germinate (DeFalco et al., 2003; Salo, 2004; Wade and Loik, 2017). This provides red brome with a large competitive advantage in sufficiently wet years as it can germinate far in advance of the native California flora allowing the red brome to dominate the ecosystem and suppress the proliferation of the native plant community (DeFalco et al., 2003). In drought years however, this germination strategy is extremely detrimental. If a minor rainfall occurs and this precipitation event is followed by a long dry period, the vast majority of brome individuals will die due to their inability to conserve water like traditional desert and semi-arid grassland plants (DeFalco et al., 2003). Furthermore, red brome seeds rapidly lose viability; red brome is incapable of performing long term seed dormancy (DeFalco et al., 2003; Salo, 2005). Therefore, increased drought frequency may actually be beneficial to native Californian plant communities as over successive drought years, red brome will experience large population declines while the native Californian flora are capable of coping with the drought and if conditions do become too stressful, seed dormancy can be utilized to avoid the extreme conditions. Native species also had a significant effect on brome mortality as brome mortality was significantly greater when grown with Phacelia, across all water treatments. This observation also supported the predictions of the present study. Phacelia is an extremely effective crop cover plant. It is highly competitive for nutrients and soil moisture and is capable of producing large amounts of aboveground biomass to shade out neighbouring plants (Killian, 2016; Turson et al., 2018). Turson et al., (2018), observed that Phacelia suppressed noxious weeds in an abandoned agricultural landscape by 75%; the greatest out of 5 cover crop species.

The suppressive effects of Phacelia were further exemplified in the brome biomass per individual observations. Native species had a significant effect on brome biomass per individual with Phacelia driving the lowest brome biomass across all water treatments. Furthermore, it was also observed that brome biomass per individual decreased across increasing water availability. This suggests that Phacelia is capable of outcompeting brome in drought conditions and this competitive advantage increases as resources become less limited. Through analyzing brome population dynamics, it would be expected that brome biomass would increase across increasing water availability as red brome is the most competitive when water is abundant and increases in red brome population size follow wetter growing seasons (Salo, 2004). However, the findings of the present study suggest that Phacelia gains a greater competitive advantage than brome under increasing water availability; the greater growth driven by larger quantities of water, increase the shading effects of Phacelia on the neighbouring brome in turn driving lower brome productivity (Turson et al., 2016).

The global models for brome biomass per individual and brome mortality, which analyzed the combined effects of native species and water availability, were not significant implying that there were no interactions between these variables.

**Implications and Conclusion**

It can be concluded that drought has negative impacts on both the growth and survival of native Californian plants. This finding poses serious questions regarding the future state of Californian native annual plant populations as IPCC reports predict that under impending climate change, the severity and frequency of drought is expected to increase over the next 100 years (IPCC AR5, 2014). The combination of increased mortality and reduced fecundity, as a result of smaller plants and below average productivity, is expected to induce rapid declines and possible extirpation of native Californian plants (Prugh, 2018). However, drought also has a significant negative impact on red brome mortality. Furthermore, unlike native Californian annuals, brome does not possess an effective drought evasion strategy (Wade and Loik, 2017; DeFalco et al., 2003). While native annual plants are capable of performing seed dormancy, thereby only germinating once conditions are favourable, red brome cannot perform such drought evasion (DeFalco, 2003). Furthermore, red brome seeds rapidly lose viability (DeFalco, 2003). Therefore, future drought severity may be a net benefit to native Californian plants as successive drought years are expected to have a greater negative impact on red brome, then on native Californian plants in turn reducing the prominence of red brome across Californian ecosystems (DeFalco et al., 2003; Salo, 2004).

Nevertheless, red brome has not only invaded drought prone ecosystems, but a wide variety of grassland and semi-arid habitats throughout California (Salo, 2004). In order to control red brome populations in these areas, human intervention and restoration tactics are clearly required. The present study revealed that out of three highly ecologically resistant native Californian annuals, *Phacelia tancetifolia* was the most effective at suppressing the success of red brome. Phacelia induced the greatest red brome mortality and the lowest red brome productivity while simultaneously maintaining relatively low mortality rates when grown in the presence of brome and the highest biomass per individual when grown in the presence of brome. These observations were consistently observed across all five water treatments. Therefore, it can be concluded that Phacelia may be a species on interest in controlling the spread of red brome as it is very successful when competing with red brome, across a wide array of environmental conditions. However, simply planting Phacelia seeds in habitats already dominated by red brome is not a successful restoration strategy. The abundance of red brome leaf litter which is left after the growing season will suppress the vast majority of Phacelia germination in turn having no reducing effect on the red brome population (Salo, 2005). A possible restoration strategy that can be employed to remove the dead brome litter prior to Phacelia seeding is a controlled burn. At the conclusion of the growing season, a controlled burn will rapidly and effectively remove all brome litter thereby clearing the way for Phacelia to be seeded. The fire will also damage and reduce the viability red brome seeds in the process in turn maximally reducing the competitors to Phacelia, enabling its proliferation and success.

In conclusion, the impending threat of increased frequency and severity of droughts is expected to negatively impact native Californian annuals. Red brome expansion also threatens the proliferation of native plant communities through causing reduced growth and fecundity. However, increased drought frequency may impose greater negative ecological impacts on red brome due to its severe drought intolerance driving reduced expansion and proliferation of red brome populations. Furthermore, *Phacelia tancetifolia* has been observed to be a very successful suppressor of red brome and must be considered in biocontrol and restoration tactics for controlling red brome populations.