

**Resource limitation versus competition with an exotic invader as drivers of the success of**

**native Californian plant species**

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## **Abstract**

Native Californian plant communities are under serious threat due to increased severity and frequency of drought in addition to the progressive expansion of invasive plant species regionally. Red brome is currently one of the most rapidly spreading invasive plants in California. With a suite of competitive traits, red brome is rapidly driving declines in native plant diversity. The present study explores the combined effects of drought and an invasive competitor (red brome) on three representative native Californian plants. It was hypothesized that drought effects and invasive species exacerbate further declines in native plant populations. The experiment was done in a controlled greenhouse setting. Five watering regimes, ranging from extreme drought to extremely wet, were introduced through controlled watering every 10 days. Brome was added to all watering levels to explore invasive species impacts. Red brome had no significant effect on native mortality but significantly reduced native productivity. Interactions between brome and drought effects only significantly effected native biomass/individual. Drought increased native mortality and decreased native productivity. Conversely, red brome mortality and biomass per individual were most negatively influenced when grown with *Phacelia*. Drought significantly increased brome mortality. The negative effect of brome on native productivity suggests that competition is likely an important factor for native species proliferation but some natives are capable of competing and negatively impacting the invasive species. Furthermore, *Phacelia* is an excellent potential species to consider for future restoration programs in arid habitats where brome is present.

## **Introduction**

California is home to one of the most diverse set of dryland ecosystems globally in terms of species richness and microclimates (Myers et al., 2000). 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 have a Mediterranean climate with hot, dry summers and mild, wet winters (Zammit and Zedler, 1994). The deserts, which are located in the southeastern most portion of the state experience 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 plant species persistence (Perez-Ramos et al., 2013). 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. That said, native plant communities in California drylands are currently under

significant threat due to two major ecological factors; 1) increased frequency and severity of drought (IPCC AR5, 2014) and 2) ecological invasion of exotic plant species (Salo, 2005).

California is estimated to possess 6000 native plant species with 2200 being endemics (Myers et al., 2000; Loarie et al., 2008). Brooks et al., (2006) define California as a centre of plant biodiversity with 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 also endemic only 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). Increased frequency of drought and the spread of invasive species in California posses a serious threat to the native biodiversity as these two factors have the potential to displace native plant species, which in turn may cause an ecological collapse of unique dryland ecosystems.

### **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 (Perez-Ramos et al., 2013). 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, that

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 deeply rooted, sclerophylls (possess small, thick, waxy leaves) persist until the winter rains return (Wade and Loik, 2017). This is a typical depiction of the seasonal ecological changes that 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 it was 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 its ecological impacts. The drought tolerant plant species of Southern California typically

employ one of three mechanisms in order to survive extended and severe 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 (Balachowski et al., 2018). They survive by storing large quantities of water-soluble proteins and carbohydrates. This aids in regulating osmotic potential and provides nutrient reserves for regrowth once the water stress is 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) 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 (Balachowski et al., 2018). 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).

Collectively, these strategies are relatively successful, but survival through a sustained, multi-year drought can be problematic.

Drought tolerant plants are capable of using 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 by the seeds (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. Consequently, understanding the sensitivity to drought by native species is a critical research topic for restoration and the protection of natives.

### **Exotic plant invasions in California**

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 (Salo, 2004). 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 have originated from Eurasia and Northern Africa; 71% (Rejmanek and Randall, 1994). The invasive species that originated from Eurasia and Northern Africa are also the most successful invasive plant species in California due to the similar climate of the Mediterranean; the invading plants are not forced to overcome a significant climatic barrier such as a novel temperature or precipitation regime (Rejmanek and Randall, 1994). The rate of introduction of exotic plant species has dramatically declined over recent decades, but the geographical ranges of established invasive plant species still continues to rapidly expand since their introduction into California (Rejmanek and Randall, 1994). This rapid expansion displaces 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. Its average height ranges from 20cm to 70cm, and it is 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 can extirpate both native annual and perennial plants in southern Californian ecosystems (Salo, 2005; Salo et al., 2006). 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 relative to native plants. This allows red brome to invest greater amounts of nutrients into biomass production and in turn it displaces 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 system 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 advantage of red brome 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 then acts as fire fuel that can increase the rate of fires in invaded habitats (Salo, 2005). 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 red brome on native Californian

ecosystems, it is a critical species for additional research regarding its response to drought and competition with native Californian plants.

### **Previous research and the present study**

The effects of drought and red brome has been analyzed previously under natural conditions. Thomson et al., (2018), showed 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), and showed 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, invasive plant cover was unaffected by native species richness. Restoration tactics for controlling the spread of invasive species must be proactive rather than reactive, because 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., (2012) 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 influences 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 analyzed the survival and productivity 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 extremely wet to extreme drought. *Plantago insularis*, *Salvia columbariae*, and *Phacelia tansyifolia* 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 the field. Although, these large scale manipulative experiments produce results which are expected to be consistent with natural conditions, there are many extraneous variables at work that 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 water availability on the growth and survival of the three phytometer species. It was hypothesized that the effects of water availability and competition with an invasive species determine the productivity and survivorship of native Californian plants. It was also hypothesized that brome success is dependent on water treatment and that some of the native species can also exert competitive effects on the invasive species. The following predictions were tested: 1) Drought and competition with an invasive species negatively impacts performance of the native species; 2) The negative effects of competition with an invasive on natives is exacerbated under drought conditions; 3) Drought will negatively impact the performance of the invasive species; 4) The response of natives to competition with brome and drought is species specific and the potential reciprocal effect of natives on brome is also species dependant. By testing three phytometer species in native-invasive mixtures, the present study examines not only how plant invasion and drought will alter Californian plant communities, but also identifies the conditions and plant communities that 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 Plantaginaceae 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). This species 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. It typically grows to a height between 10cm and 50cm and produces 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 tanacetifolia* (*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 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 design**

The experiment was a fully factorial randomized 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 including a brome present and a brome absent treatment with 50 pots for each treatment, of the 100 dedicated to each native treatment. Finally, there were 5 watering regimes (10 replicates per treatment level). 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 an extremely wet year based on precipitation data collected from the San Joaquin Valley, California (Borders et al., 2011). 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 the following soil mixture: 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 cycle 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 instances were applied. Pots were given a fixed volume of water based on their respective drought treatment. The precipitation measurements obtained were based on a standard 2cm radius National Weather Service rain gauge and therefore had to be converted to the proportional water volume calculated for a 78.54cm<sup>2</sup> circle of surface area that would receive rain (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 (Schneider et al., 2014). These values were divided by 6 (the number of watering periods) to determine the volume per watering instances per pot.

### **Data collection**

Three censuses 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. These census data were 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, five measurements were taken for each pot; total aboveground biomass per species, percent soil moisture, germination rate per species, mortality rate per species, and mean biomass per individual plant present. 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 that would have been introduced by probe placement and insertion into the pots. 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 an SM-150 Delta Technologies AT Soil Moisture Kit accurate to one decimal place.

Germination rate per species was calculated by taking the number of individuals of each species in each pot at census 1 and dividing by 10 (the number of seeds per species). Mortality rate per species per pot was calculated using the equation [1 - Proportional Survivorship at Census Three]. This calculation defines mortality as all individuals that did not germinate or germinated but did not survive to the conclusion of the experiment. The third census was set as the plant establishment life stage to ensure that all the seeds that were likely to germinate in this experiment had an opportunity to do so. Mean 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 mean productivity investment per individual per species across all 300 replicates.

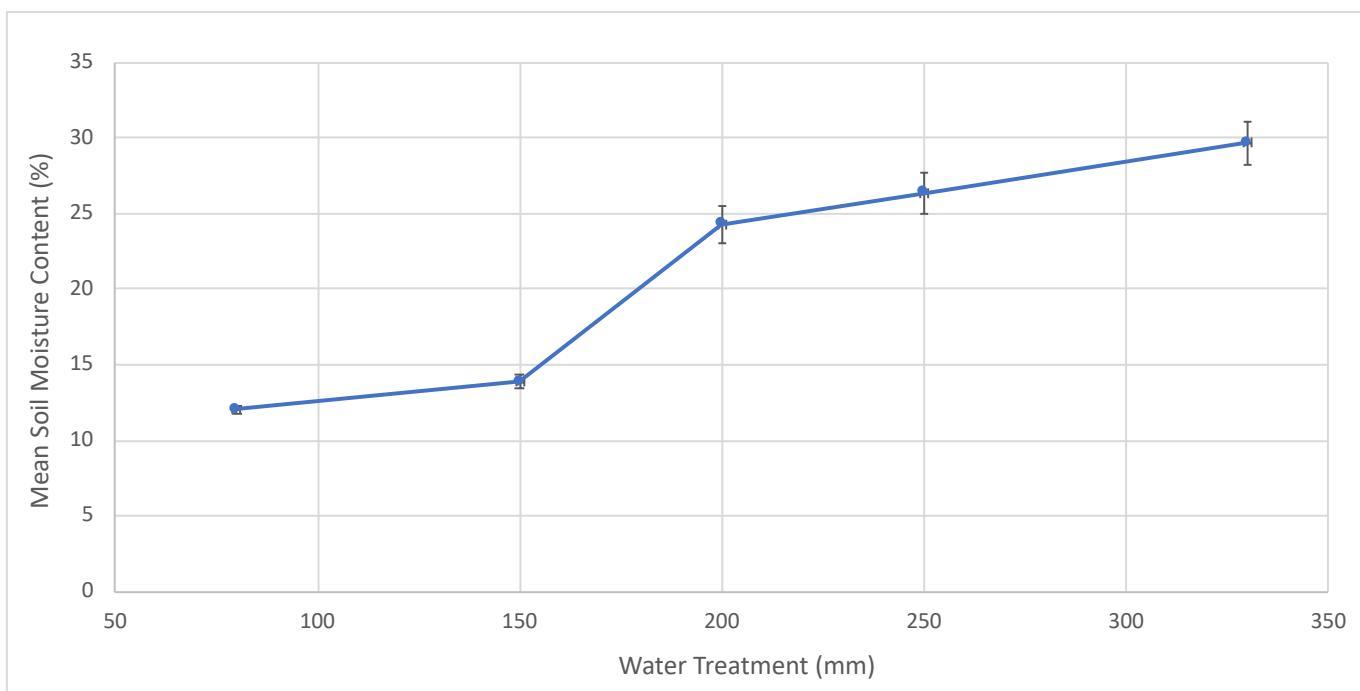
## **Data analysis**

General linear models (GLM) were utilized to examine native and brome germination, mortality and biomass per individual across water treatments. Tukey LSD post-hoc Tukey tests were applied to identify differences between native species and across the water treatments. Independant sample t-tests were also used to determine if native germination, mortality and productivity was significantly different with and without brome across each of the five water treatments. Finally, six global GLMs were performed to analyze if there was significant interaction between the independent variables (native species identity, water treatment, and brome treatment) in determining native and brome germination, mortality and productivity. All statistical procedures were performed in SPSS version 24.

## **Results**

### **1) Confirmation of water treatment effects on soil moisture**

The water treatments followed a pattern of increasing soil moisture across increasing levels of precipitation [Figure 1]. The 80mm and 150mm treatments were significantly different from all other water treatments [Table 1], and therefore accurately simulated the watering regime of a drought. The 200mm treatments was different from all other watering regimes [Table 1] 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 [Table 1].



**Figure 1)** Mean soil moisture content across the five water treatments. The measurements were averaged across all 60 pots set at each of the five water treatments. Error bars represent the mean plus/minus the standard error.

**Table 1)** Statistical output of P-values from post-hoc Tukey tests comparing differences in soil moisture between the 5 watering treatments. Significant differences are denoted by P-values less than 0.05.

Water Treatments	80mm	150mm	200mm	250mm	330mm
80mm		0.746	P<0.001	P<0.001	P<0.001
150mm	0.746		P<0.001	P<0.001	P<0.001
200mm	P<0.001	P<0.001		0.032	0.004
250mm	P<0.001	P<0.001	0.032		0.196
330mm	P<0.001	P<0.001	0.004	0.196	

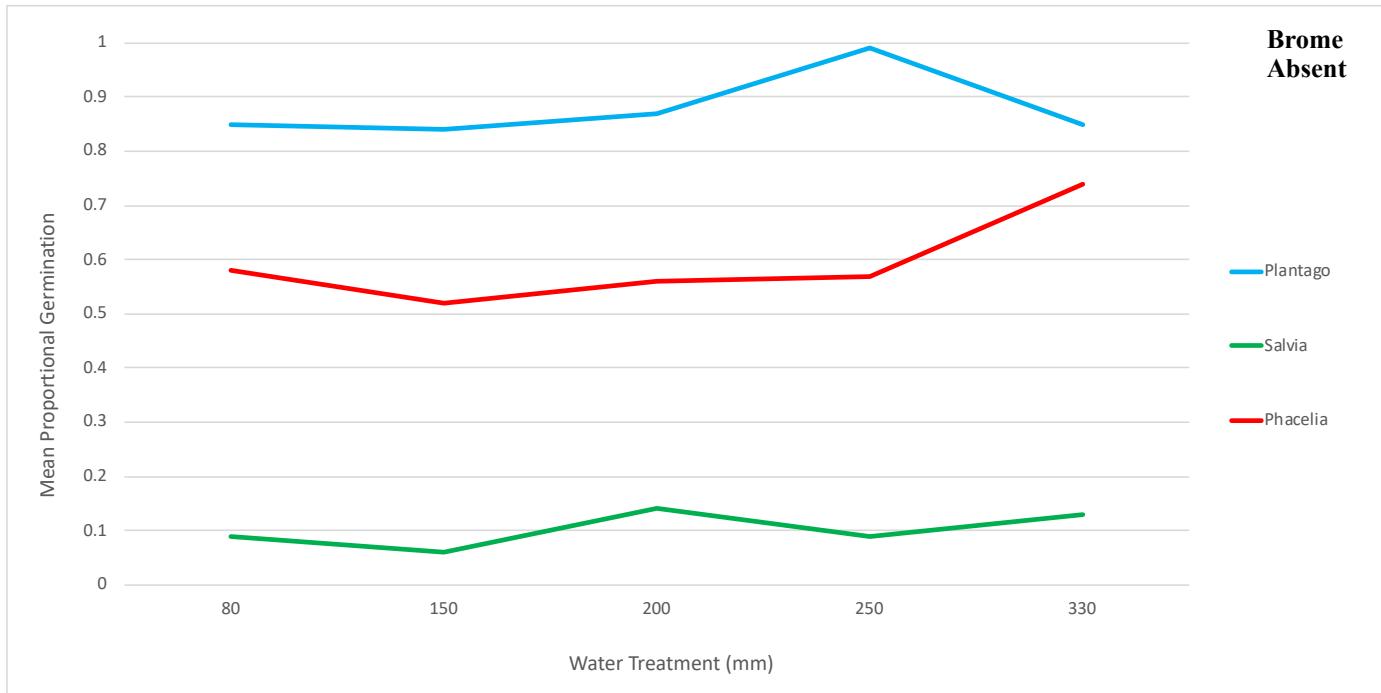
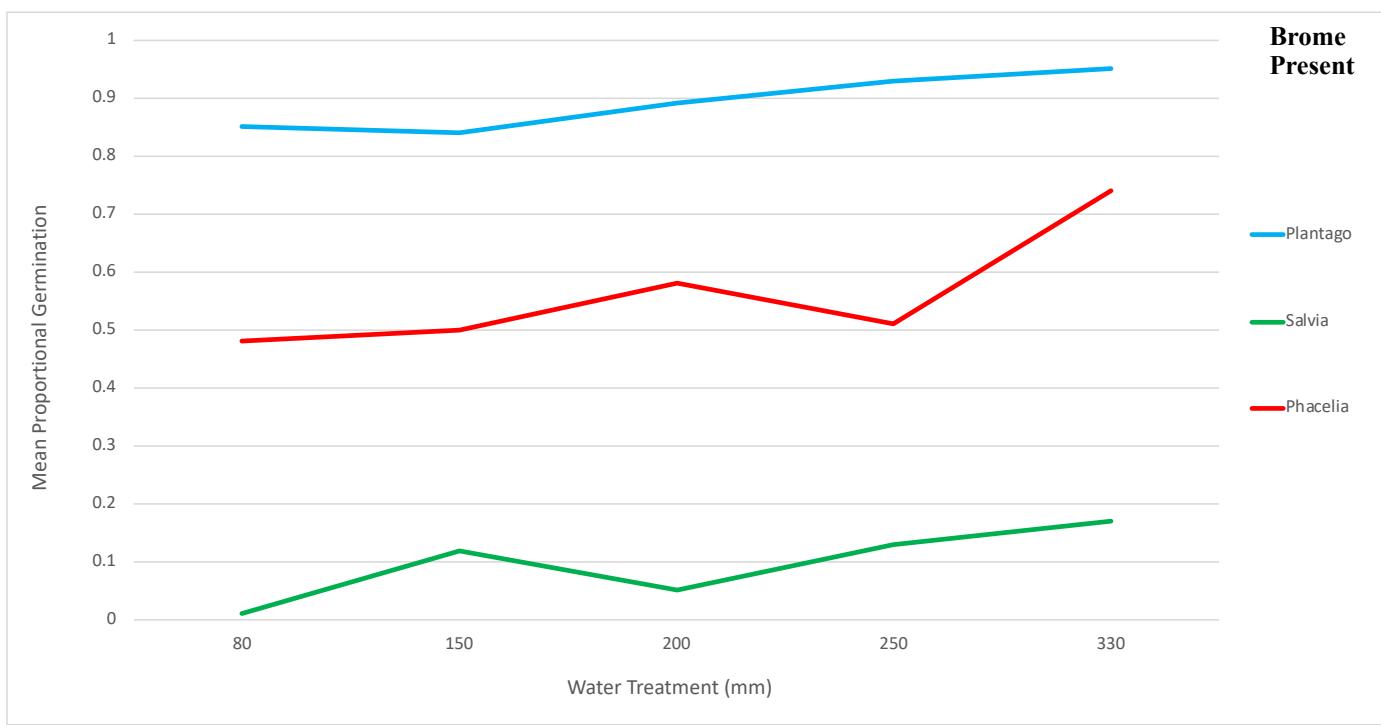
## **2) Native responses to drought and competition**

The germination rates of the three native species were significantly different from one another, across all treatments [Table 2A, Figure 2]. *Plantago* had the greatest germination rates across all treatments ( $P<0.001$ ), while *Salvia* possessed the lowest germination rates across all treatments ( $P<0.001$ ). Water availability did not significantly enhance native germination [Table 2A, Figure 2], and brome presence also did not have a significant effect on native germination [Table 2A, Figure 2]. There were no significant interaction terms in determining native germination.

Native species mortality responses were species specific and water treatment had a significant effect on native mortality [Table 3A]. Brome did not have a significant impact on native plant mortality [Table 3A]. *Plantago* had the lowest mortality ( $P<0.001$ ) and *Salvia* had the greatest mortality ( $P<0.001$ ) [Figure 3]. Native mortality for all three species was not significantly different when grown with and without brome [Table 3A]. *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 ( $P = 0.147$ ) [Figure 3]. There were no significant interaction terms in determining native mortality [Table 3A].

Species identity, water availability and brome all significantly influenced mean native biomass per individual [Table 4A, Figure 4]. *Phacelia* had the greatest biomass/individual ( $P<0.001$ ) while *Salvia* possessed the lowest biomass/individual ( $P<0.001$ ) [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 significantly greater between the brome and no brome treatments at the 330mm water treatment ( $P = 0.007$ ). *Plantago* had significantly lower biomass/individual at the 80mm and 150mm treatments when grown with brome (80mm:  $P = 0.007$ ; 150mm:  $P = 0.016$ ). *Salvia* had significantly lower biomass/individual with brome at the 80mm treatment (80mm:  $P = 0.006$ ). The interaction term between all three independent variables was significant, however there was no significant interaction when only two of the variables were analyzed at a time [Table 4A].

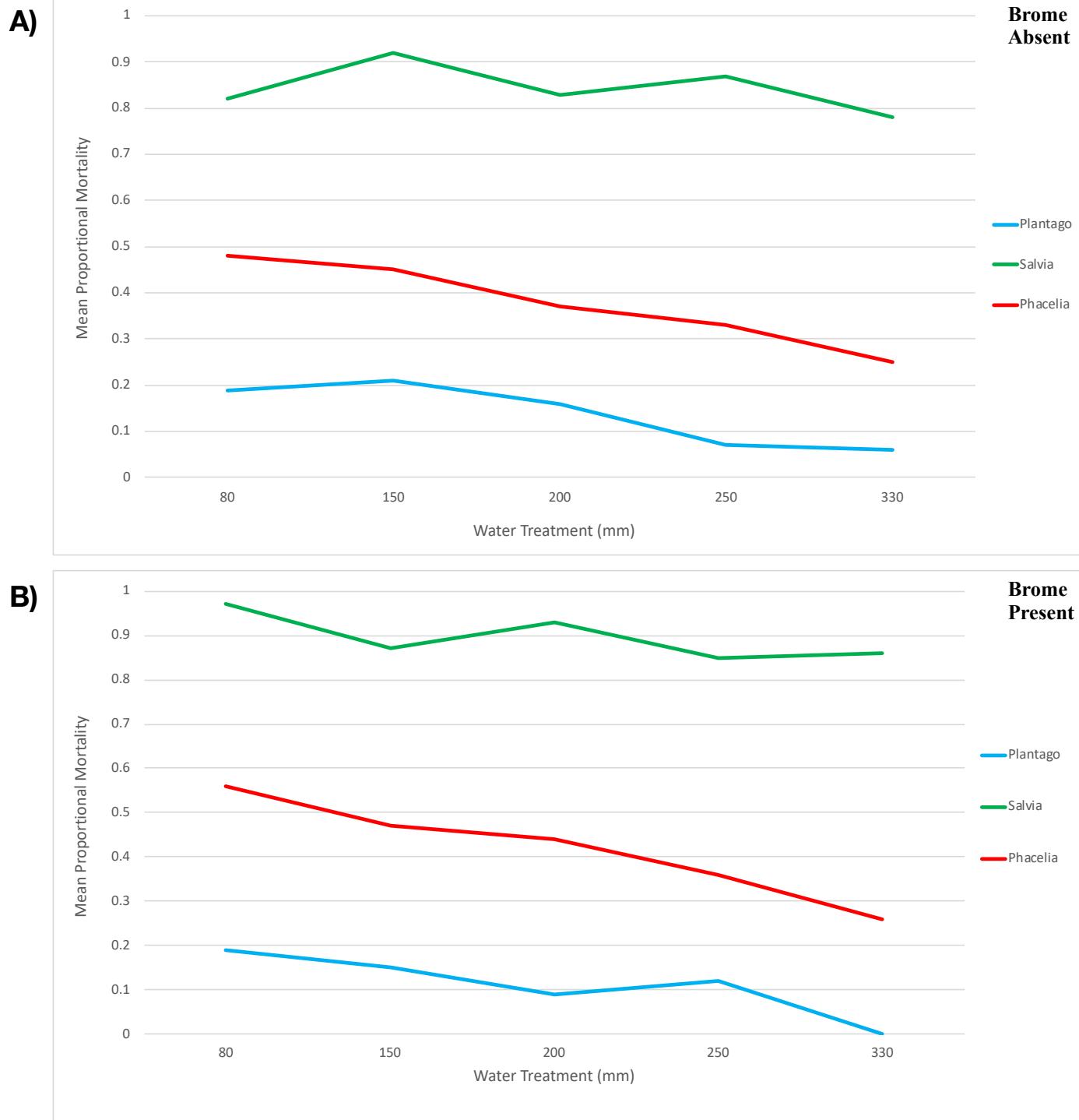
**A)****B)**

**Figure 2)** Mean germination of each native species across the five water treatments A) when grown in the absence of brome and B) when grown in the presence of brome. Germination is represented as the proportion of the 10 seeds planted in each pot, that germinated by the first census.

**Table 2)** General linear model testing of the effects of water treatment, native species identity and brome treatment on A) native germination and B) brome germination. df represents degrees of freedom.

A)	Model	df	F-Value	P-Value	Effect Size
	Water Treatment	4	1.108	0.353	0.082
	Native Species	2	658.071	P<0.001	0.83
	Brome Treatment	1	0.236	0.628	0.001
	Brome Treatment X Native Species	2	0.512	0.6	0.004
	Brome Treatment X Water Treatment	4	1.031	0.392	0.015
	Water Treatment X Native Species	8	1.015	0.36	0.059
	Brome Treatment X Native Species X Water Treatment	8	0.627	0.755	0.018
	<b>R<sup>2</sup> = 0.817</b>				

B)	Model	df	F-Value	P-Value	Effect Size
	Water Treatment	4	1.167	0.328	0.033
	Native Species	2	2.501	0.064	0.049
	Water Treatment X Native Species	8	0.742	0.654	0.042
	<b>R<sup>2</sup> = 0.024</b>				



**Figure 3)** Mean mortality of each native species across the five water treatments A) when grown in the absence of brome and B) when grown in the presence of brome. Mortality is represented as the proportion of the 10 seeds planted in each pot that either did not germinate by, or survive until, the third census.

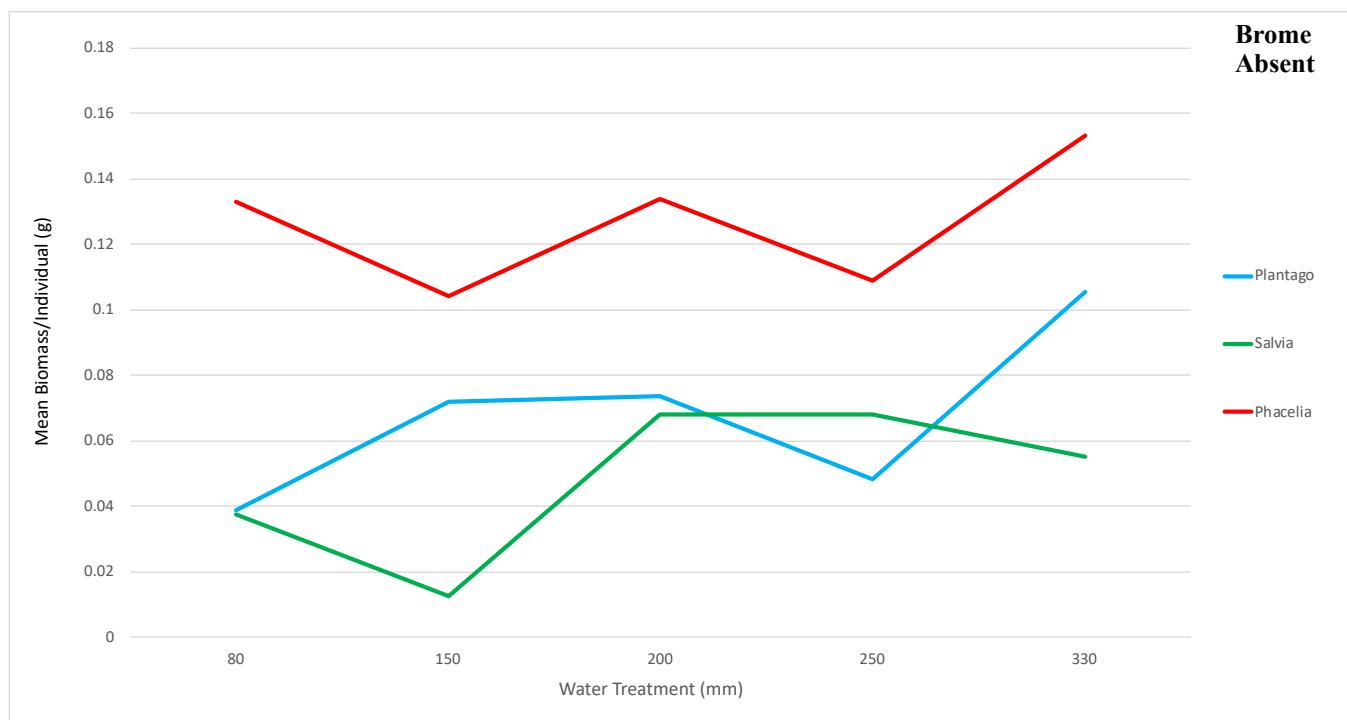
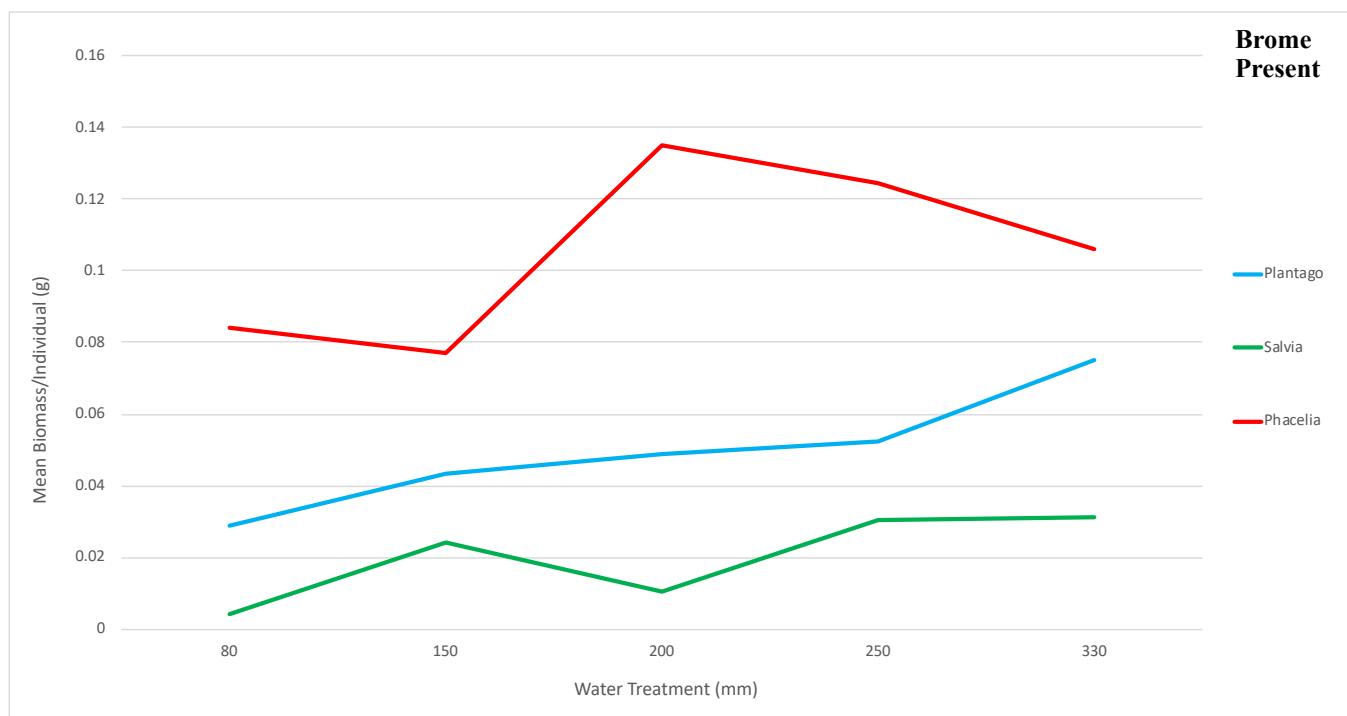
**Table 3)** General linear model testing of the effects of water treatment, native species identity and brome treatment on A) native mortality and B) brome mortality. df represents degrees of freedom.

A)

Model	df	F-Value	P-Value	Effect Size
Water Treatment	4	14.436	P<0.001	0.176
Native Species	2	786.12	P<0.001	0.853
Brome Treatment	1	2.003	0.158	0.007
Brome Treatment X Native Species	2	2.621	0.075	0.019
Brome Treatment X Water Treatment	4	1.235	0.296	0.018
Water Treatment X Native Species	8	1.494	0.159	0.042
Water Treatment X Native Species X Brome Treatment	8	0.86	0.551	0.025
<b>R<sup>2</sup> = 0.845</b>				

B)

Model	df	F-Value	P-Value	Effect Size
Water Treatment	4	11.837	P<0.001	0.26
Native Species	2	16.665	P<0.001	0.198
Water Treatment X Native Species	8	1.184	0.313	0.066
<b>R<sup>2</sup> = 0.338</b>				

**A)****B)**

**Figure 4)** Mean biomass per individual of each native species across the five water treatments A) when grown in the absence of brome and B) when grown in the presence of brome.

**Table 4)** General linear model testing of the effects of water treatment, native species identity and brome treatment on A) native biomass per individual and B) brome biomass per individual. df represents degrees of freedom.

A)

Model	df	F-Value	P-Value	Effect Size
Water Treatment	4	8.46	P<0.001	0.111
Native Species	2	118.123	P<0.001	0.467
Brome Treatment	1	25.379	P<0.001	0.086
Brome Treatment X Native Species	2	2	0.633	0.003
Brome Treatment X Water Treatment	4	4	0.249	0.02
Water Treatment X Native Species	8	8	0.053	0.055
Brome Treatment X Native Species X Water Treatment	8	8	0.032	0.06
<b>R<sup>2</sup> = 0.505</b>				

B)

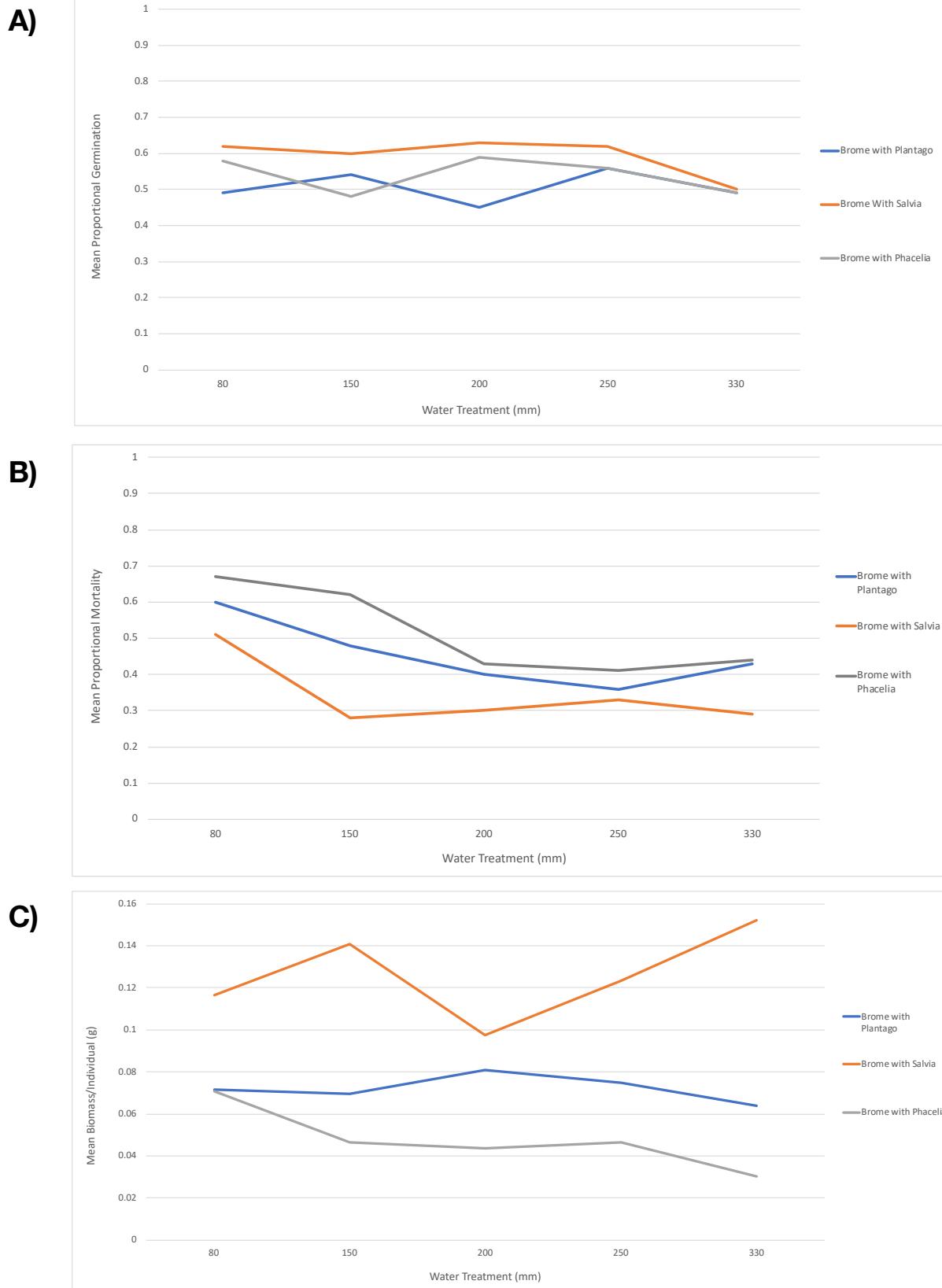
Model	df	F-Value	P-Value	Effect Size
Water Treatment	4	0.246	0.912	0.007
Native Species	2	27.74	P<0.001	0.291
Water Treatment X Native Species	8	1.09	0.374	0.061
<b>R<sup>2</sup> = 0.256</b>				

### **3) Brome responses to drought and competition with natives**

Brome germination did not vary significantly when grown with the different native species or across water availability [Table 2B; Figure 5A]. There were no significant interaction terms in determining brome germination [Table 2B].

Brome mortality varied across the different native species and it was negatively impacted by drought [Table 3B; Figure 5B]. *Phacelia* induced the greatest brome mortality ( $P < 0.001$ ) and *Salvia* induced the lowest brome mortality ( $P < 0.001$ ) [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]. There was no significant interaction terms in determining brome mortality [Table 3B].

Mean brome biomass per individual was significantly affected by native species identity while drought did not significantly influence mean brome biomass per individual [Table 4B]. *Salvia* reduced brome biomass the least ( $P < 0.001$ ) and *Phacelia* reduced brome biomass the greatest ( $P = 0.012$ ) [Figure 5C]. 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, these trends were insignificant. There was no significant interaction terms in determining brome biomass per individual [Table 4B].



**Figure 5)** Mean A) germination, B) mortality, and C) biomass per individual of brome when grown with the three native species, across the five water treatments. Germination and mortality are represented as proportions of the 10 seeds which were initially planted in each pot.

## **Discussion**

Drought and competition with invasive species are fundamental challenges to the functioning and biodiversity of drylands globally. In California, drought and invasion by red brome pose a serious ecological threat and in the current study, the relative importance of both variables on representative natives species was tested. The hypothesis that drought and competition influence key measures of success for native plants was supported for all measures. It was also supported that brome success is impacted by both native species identity and water availability. The prediction that drought and competition with an invasive species negatively impacts native species productivity and survivorship was supported. However, drought only exacerbated the negative effects of competition with an invasive species in regards to native biomass per individual, not mortality. The prediction that brome experiences reduced success under drought conditions was also supported. Finally, the prediction that the response of natives to competition with brome and drought is species specific and the potential reciprocal effect of natives on brome is also species dependant was also supported.

### **Drought effects on natives**

Water availability is the key abiotic variable that determines the proliferation of plant communities in arid ecosystems (Perez-Ramos et al., 2013). Water availability significantly affected native mortality but not native germination. The germination of desert annuals is induced by precipitation and increased soil moisture (Keeley, 1991), ensuring that growth coincides with the onset of winter rains. Rates of germination tend to increase with increased size of the initial precipitation event (Wade and Look, 2017), contrasting with the findings of the present study. However, fast pulses of both small and large precipitation events (like those

simulated in the present study) have been observed to stimulate the germination of desert annuals at relatively similar rates (Levin et al., 2011; Harrison et al., 2017). The negative impacts of the lower levels of precipitation are not observed until later in the growing season (Levine et al., 2011). In the present study, *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 (Savi et al., 2016; Marushia and Allen, 2011; Emery, 2016). *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 (Cox and Allen, 2008; Toth and Huse, 2014). Poor seed quality is theorized to have been the cause for high *Salvia* mortality.

Water availability significantly affected 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 growth 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).

### **Effects of competition with an invasive on natives**

Currently, red brome is one of the greatest biotic threats facing native plant communities in Californian dryland ecosystems (Salo, 2005). The mortality and germination 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 by 73% to 99% (Young et al., 2015). Brome has also been observed to reduce the survival of forbs by up to 75% in 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., (2006) observed similar results as the present study, with emergence and survival of native species being insignificantly affected by the presence of red brome. Salo et al., (2006) 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., 2006). Furthermore, many exotic plant species become invasive, not through directly outcompeting the native species but through taking advantage of favourable environmental conditions (Gill et al., 2018). In the present study, brome and the native species germinated at similar times preventing brome from suppressing the

germination and proliferation of the native species. In natural invaded sites, red brome seed density is also much greater than native seed density (Salo et al., 2006), 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. There were no significant interaction terms between drought treatment and brome presence, displaying that that competitive effects of brome do not exacerbate native morality or germination under drought conditions.

Brome significantly reduced native biomass per individual. Salo et al., (2006) observed similar results with red brome reducing native biomass per individual by 72% to 89%. A reduction in biomass is linked to reduced plant height and fecundity at the conclusion of the growing season (Salo et al., 2006). This poses a serious threat to the long term persistence of native Californian plant communities. 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., 2006). Furthermore, interaction terms between drought treatment and brome presence were significant in determining native biomass per individual with the negative effects of brome on the natives being exacerbated under drought conditions. This is consistent with the findings of Mason et al., (2012), who observed that native species were poor competitors with an exotic invader when exposed to severe water stress. As the water stress was alleviated, native species productivity increased and negative effects of competition with the

invasive species were reduced. Water treatment had a greater effect size than brome treatment displaying that drought effects are a greater threat to native species productivity than competition with an invasive species.

### **Native species specificity**

Desert annual species possess varying life history traits resulting in unique, species specific responses to environmental changes. *Plantago*, possessed the greatest germination and lowest mortality across all treatments. 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 lifecycle 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 cool temperatures (Clauss and Venable, 2000; Barron-Gafford et al., 2013). This ability to perform late-season germination may have induced a lower mortality rate for *Plantago* as new individuals could have sprouted throughout the experimental period. 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* possessed the greatest biomass per individual across all treatments. 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). These observations suggest that *Phacelia* can optimize growth under a wide array of environmental conditions and plant assemblages.

### **Brome response to treatments**

In order to adequately control further proliferation of red brome, it is essential to understand how it responds to environmental changes within particular plant communities. Water availability and native species identity had a significant effect on brome mortality but did not affect brome germination. Drought conditions drove significantly greater brome mortality; an observation consistent with previous research. 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, over successive drought years, red brome is expected to 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 (DeFalco et al., 2003; Balachowski et al., 2018). Native species also had a significant effect on brome mortality as brome mortality was significantly greater when grown with *Phacelia*, across all water treatments. *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, with *Phacelia* driving significantly lower brome biomass per individual across all water treatments. This suggests that *Phacelia* is capable of outcompeting brome in both drought conditions and extremely wet conditions. There were no significant interaction terms between native species identity and water treatments in determining brome germination, mortality, or biomass per individual displaying that there are no significant interaction effects.

### **Conservation implications**

The data suggests that drought may negatively affect the growth and survival of native Californian plants more than competition with a dominant exotic invader. 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). The negative impacts of drought on native species is exacerbated by competition with red brome which will only lead to more rapid population declines in red brome invaded habitats.

However, 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). Therefore, future drought severity may reduce the prominence of red brome across Californian ecosystems (DeFalco et al., 2003; Salo, 2004). This is expected to reduce the stress competition experienced by native plant

communities but the resource limitation threat imposed due to drought is still a major challenge impeding the proliferation of plant communities in California dryland ecosystems (Prugh, 2018).

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 required. The present study revealed that out of three highly ecologically resistant native Californian annuals, *Phacelia tanacetifolia* 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 of 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 (Chen et al., 2018; 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.

## **Conclusion**

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 tanacetifolia* has been observed to be a very successful suppressor of red brome and must be considered in conservation efforts to restore native biodiversity to invaded ecosystems.

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## Appendix



1) Experimental setup immediately after seeding.



2) Pots after 2 months of growth.



3) *Plantago insularis* with flowers blooming



4) *Phacelia tanacetifolia*



5) *Salvia columbariae*

**Source:** <https://medivetus.com/botanic/salvia-columbariae-chia-edible-and-medicinal-uses/salvia-columbariae-7/>



6) *Bromus madritensis* subspecies  
*rubens*

**Source:** [https://www.inaturalist.org/guide\\_taxa/493086](https://www.inaturalist.org/guide_taxa/493086)