Title

Germination Characteristics of Coastal Sage Scrub Plant Species

Author

Garrambone, Matthew Scot

Publication Date

2018

UNIVERSITY OF CALIFORNIA,
IRVINE

Germination Characteristics of Coastal Sage Scrub Plant Species

THESIS

submitted in partial satisfaction of the requirements
for the degree of

MASTER OF SCIENCE

in Ecology and Evolutionary Biology

by

Matthew Scot Garrambone

Thesis Committee:
Professor Travis Huxman, Chair
Professor Diane Campbell
Professor Kailen Mooney
Project Scientist Sarah Kimball

2018

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ABSTRACT OF THE THESIS

Germination Characteristics of Coastal Sage Scrub Plant Species

By

Matthew Scot Garrambone

Master of Science in Ecology & Evolutionary Biology

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Professor Travis Eugene Huxman, Chair

The extent to which patterns of germination are influenced by the environment is mediated by germination functional traits related to both temperature and water potential. The co-variance of these traits informs our understanding of how these organisms cope with periods of environmental stress, such as drought. Here we quantify the effect of variation in temperature and water potential on germination for nine coastal sage scrub plant species representing multiple life forms, using a growth-chamber based hydrothermal approach, and compare the results to traits known to relate to growth and water use. We also assess the potential of germination, growth, and water-use traits to inform our understanding of how coastal sage scrub vegetation responds to water limitation in Southern California. We investigated how both regenerative and vegetative traits may influence the evolution of plant life history strategies in this complex and dynamic system. We identified relationships between germination fraction, base water potential required for germination, and water-use efficiency. Specifically, we find that species with low base water potential ($\psi_b(50)$) have high water use efficiency (WUE), low thermal time to germination (θ_T) , and germinate high fractions, while those with high

$\psi_b(50)$ have low WUE, high θ_T and germination low fractions. Species differences in traits related to water sensing and water-use served as effective predictors of how percent-cover of vegetation changed during a three-year drought period. We found that native plant species which increased cover during drought germinated high seed fractions, had low base water potentials, and were more water-use efficient compared to those that avoided drought through sets of functional traits that related to the life history tactic of escape. Overall, our study helps to further our understanding of plant strategies associated with environmental variation by highlighting key functional traits that may confer tolerance to environmental stress

INTRODUCTION

How the life cycle components underlying regeneration of plants are affected by environmental variation informs the evolution of plant life history strategies, population dynamics, and community assembly (Grime 1981, Lambers et al. 2008, Donahue et al. 2010, Fraaije, et al. 2015). Seed germination must be timed to occur when environmental conditions (light, oxygen, temperature, and moisture) are favorable (Baskin & Baskin, 1998). The timing of germination must be coordinated within periods of the growing season that allows for successful establishment and subsequent vegetative performance (Baskin & Baskin 2004, Fenner & Thompson 2005). In variable environments characterized by unpredictability in primary drivers such as precipitation, extended periods when conditions are optimal to support germination and establishment may be rare (Lambers et al. 2008). How traits associated with seed germination for different species are adapted to this uncertainty, and how those adaptations influence regeneration, has long been studied by scholars, though we are still building a full understanding of this key life stage (Grubb 1977, Fenner 2000, Poshlod 2013, Jimnez-Alfaro et al. 2016).

In variable environments, plant strategies aimed at reducing variance in fitness help facilitate species persistence and co-existence (Venable & Lawlor 1980, Venable & Brown 1988, Chesson & Huntly 1989, Angert et al. 2009). Germination cueing and seed dormancy, two strategies that work to optimize germination timing, have been shown to buffer desert annual populations against inter-annual variation (Cohen 1966, Pake & Venable 1996, Venable & Brown 1988, Gremer & Venable 2014). These strategies potentially delay germination and effectively “bet-hedge” against the risk of failure by distributing a fraction of the seed population through time by forming a persistent seed bank (Walck et al. 2005, Venable 2007). Germination functional traits related to temperature and water potential mechanistically underlie these germination patterns, and along with physiological traits associated with growth and water-use, strongly predict long-term population and community dynamics for the one system studied in depth (e.g., Huang et al. 2016). While science has developed a good understanding of germination ecology in relatively straight-forward settings, to the best of our knowledge, such principles have not been translated to ecosystems with greater complexity in life form or environmental context.

To extend the developing concepts of germination ecology, we evaluated functional traits underlying germination for a suite of species with different life forms in a well-studied Mediterranean ecosystem in North America. Our study contrasted species in their germination characteristics within the semi-arid southern California coastal sage scrub (CSS) community characterized by drought-deciduous perennial shrubs that co-occur with a dynamic assemblage of perennial forbs, perennial grasses, and herbaceous annual forbs (Rundel 2007, Westman 1982, Keeley 1984). In this system, regeneration of plant communities from seed occurs both in close association with disturbance by fire and during the extended intervals between fire (Westman 1982, Keeley 1984, DeSimone 1999) when community species composition dynamically changes (Westman 1982).

In this system, life history syndromes associated with the regeneration phase have been described for fire adapted response, where a large group of refractory species, primarily herbaceous annuals, possess fire associated seed dormancies that prevent germination until the first and second year rains following a fire event (Keeley 1991). There is little evidence that perennials occupy the persistent soil seed bank, though they likely are present in transient forms, where they may rapidly lose dormancy through after-ripening in the summer following dispersal, then germinate with subsequent winter rains (Cox & Allen 2008, Boyd et al. 2009, DeSimone, 1999, Keeley 1991), or by inference, when they fail to germinate, have short lifespans in the soil. Non-refractory species, those that do not possess fire associated dormancies, including some herbaceous and woody perennial species, primarily regenerate by crown-sprouting post fire, and often do not recruit by seed until the second year following disturbance (Westmann 1981, Keeley & Keeley 1984, Malanson 1984, Malanson & Westmann 1985). Between fire events, species richness of herbaceous annuals declines, and that of herbaceous, drought deciduous, and woody perennials increase (Keeley 1984, Keeley 2005, Kimball 2014). We know the composition of the resulting community is largely driven by precipitation in the first years following disturbance (Keely 2005) but its specific influence on germination is yet undefined.

Regional and microsite environmental conditions strongly influence germination response (Kimball et al. 2010, Keeley 2005, Walck et al. 2011, Adler & Hille Ris Lambers, 2008). Temperature and soil moisture, specifically, strongly influence germination dynamics in arid systems (Mott 1974, Flores & Briones 2001). Here we use a hydrothermal time approach (e.g., Gummerson 1986, Dahal and Bradford 1994, Finch-Savage et al. 1998) to quantify the influence of two primary germination drivers—temperature and water potential—on seed germination, in an effort to better understand the germination dynamics of species in this semi-arid southern California CSS system. Hydrothermal time assessments use time-series of experimental germination in different water and temperature combinations to determine hydrothermal time, a measure of progress towards germination, measured in Mega-pasqual degree days (MPa ° d), T_b - the base temperature below which germination does not occur, T_c - the temperature above which germination does not occur, and $\psi_b(g)$ - the minimum water potential (ψ) required for germination of the g fraction (an arbitrary percentage of the seed population, typically evaluated at 50%). We examine relationships between these germination characteristics and other functional and morphological variables we expect to be important in this system (e.g., seed mass, relative growth rate (RGR), and water use-efficiency (WUE)) (Thompson et al 1993, Huxman 2013, Gremer 2013). We also explore whether a better understanding of germination functional traits associated with CSS species may help to predict how these species may respond to environmental variation, such as the extended periods of drought in the contemporary record.

We hypothesize that patterns of germination trait co-variation identified in other water limited ecosystems will also be observed in this water-limited, Mediterranean setting. We expect low germination fractions, high thermal time to germination (θ_T), less negative $\psi_b(50)$, and low T_b and T_c to be associated with annual forbs that rely on 'escape' in the face of environmental stress and the requirement to only germinate under conditions favoring establishment of seedlings and subsequent adult performance. Extending from the findings of Huang et al (2016), we expect drought deciduous perennial shrubs in this system will germinate high fractions, and possess low θ_T requirements, more negative $\psi_b(50)$, and high

T_b and T_c, facilitating opportunistic germination across a range of conditions, as a result of their relatively greater reliance on vegetative strategies to persist through environmental stress.

In addition, we expect coordination among germination and vegetative traits (i.e., Huang et al., 2016). We expect germination characteristics related to slow, or delayed germination, to correlate with low WUE, described here by high Δ^{13}C (integrated WUE measured as carbon isotope discrimination) and high RGR. Conversely, we expect those species with high germination fractions, $\psi_b(50)$ and low θ_T to have high WUE (low Δ^{13}C) and low RGR (Angert 2007, Huxman 2013, Huang et al 2016). Additionally, we hypothesize that traits related to sensing or using water: $\psi_b(50)$ and WUE, will serve as effective predictors for which species increased vegetative cover during a three-year drought period where we documented species performance (Kimball 2017). Such information will help us to predict how populations may respond to future droughts, understand the consequences of the hotter and drier Southern California environment predicted by future climate models, and help inform conservation and ecological restoration efforts in this highly fragmented and degraded system (Kimball 2017, Chornesky 2015, Merritt & Dixon 2011).

Materials and Methods

Germination traits

We examined germination traits for 9 coastal sage scrub species (Table 1). Seed was collected in 2015-2015, from established plots at a native seed farm operated by the Irvine

Ranch Conservancy, in Irvine, CA. Seed was collected from a minimum of 750 individual plants of each species at the seed farm. Collections were combined, processed, and then transferred to poly-weave bags. Seed was after ripened for 3-4 months under ambient field conditions (Irvine Ranch Weather Station) then placed in a climate-controlled seed storage container until 3 weeks prior to study period. Storage conditions were a constant 7°C and 35% RH. For each species, the seeds included in the study were selected at random from the combined total collection.

For each species, seed germination trials were conducted in petri dishes in four growth chambers (Percival E41HO) at four constant temperatures: 8°C, 14°C, 22°C, and 28°C. Within each chamber species were exposed to four water potentials: -0.025 MPa, -0.135 MPa, -0.325 MPa, -0.5 MPa. Water potential was controlled by PEG8000 solution, prepared according to Michel (1983). Seeds were incubated on two layers of filter paper (Whatman 70mm) - with a pin hole poked in the top layer - and moistened with 1.5 mL of PEG solution in plastic 80mm petri dishes. Petri dishes were wrapped in Parafilm to reduce evaporation, and solutions in each dish were renewed every 48 hours to maintain constant water potentials. Solution were renewed by removed excess solution with a plastic pipette and replacing with 1.5 mL of the appropriate PEG solution.

Germination trials were conducted on a total of eight replicates for each treatment combination, with replicates divided into two groups of four that were germinated in different chambers to reduce potential chamber effects. The number of seeds sown into each petri dish (Table 1) were selected based on seed viability assays for these seed populations, performed by MD Seed Labs Santa Barbara, CA. The majority of viability assays were performed using tetrazolium chloride staining, though in some cases a second trial was conducted on un-germinated seeds after pre-treatment using gibberellic acid (GA3). The number of seeds per dish varied by species in an effort to provide a minimum of 10 viable seeds per dish. Dishes were arranged randomly on clear plastic trays and two trays were placed in each growth chamber under constant temperatures in light. Dishes were rotated after each germination observation (~ each day) to minimize any position effects in the chambers. Germination was scored as radical emergence and was recorded every 24 hours for the first 14 days of the study, and every 48 hours for the remainder of a 30-day period.

Growth and water-use traits

Vegetative traits associated with growth and water-use were collected from two-year-old plants established in irrigated common garden plots at the Conservancy's seed farm. To determine relative growth rate (RGR) 4 one-year old plants were sampled in time for each of our seven species during the 2014-2015 growing season. Approximately bimonthly (five-seven points in the growing season), marked individuals were measured to estimate size. Plant height and width in two axes were determined to estimate volume, which correlates with mass in these species. Plants were separated by tissue type – roots, stems, leaves, and flowers – and dried at 65°C to determine biomass for the respective tissues. RGR was determined using the slope of the line obtained from plotting the natural log of the mean total biomass at four-time points beginning at germination.

Carbon isotope discrimination ($\Delta^{13}C$) was determined using three dried leaves from each plant, which were ground to a fine powder and analyzed at UC Irvine's Stable Isotope Ratio Mass Spectrometry Lab (IRMS) lab using mass spectrometry. In addition to D13C, tissue was analyzed for %N, %C, and C:N. Carbon isotope discrimination is a good proxy for integrated water-use efficiency. Discrimination values were calculated as in Farquhar (1989):

$$\Delta = (\delta a - \delta p)/(1+\delta p/1000) \qquad (1)$$

Where δa and δp are the carbon isotope ratio in the atmosphere (assumed 8 ppm; $^{o}/_{oo}$) and in the leaf respectively.

Drought response measurements

From 2012-2015 percent vegetative cover of eight species was collected from 24 points in each of 1000 5 x 5 m plots from both north and South facing slopes at the West Loma Ecological Restoration Experiment during the peak of the growing season (as described in Kimball et al., 2017). Mean annual precipitation data was collected from Irvine Ranch weather: Western Regional Climate Center) and used to determine growing season precipitation (October – April) for each season. Growing season precipitation was 51 cm in the 2010-2011 season, and subsequently dropped to 17 cm (2011-12), 12 cm (2012-13), and 17 cm (2104-15). For each species, log response ratios were calculated that describe the effect of the 11-12 to 14-15 drought on percent vegetative cover (as described in Kimball et al., 2017). We use those log response ratios to address our question of whether drought response can be predicted using knowledge of germination and physiological growth traits.

Hydrothermal Modeling Approach

Temperature and water potential are known to influence germination dynamics (Roberts 1988, Fenner & Thompson 2005, Baskin & Baskin 2014, Merritt 2007, Rowse & Finch-Savage, 2003). Hydrothermal time modeling has been used to quantify the effect of temperature and water potential, and has been used to successfully model germination, seed dormancy, and after ripening in numerous species (Bradford 1990, Alvarado & Bradford 2002, Bauer 1998, Christensen 1996, etc.). However, only recently has this approach been used to compare native plant species in an ecological context (Allen, 2000, Flores & Briones 2001, Huang et. al, 2016).

The model is based on the concepts of thermal time (θ_T) and hydrotime (θ_H). θ_T represents the time between imbibition and the germination of a specific fraction of the seed population (t_g, where g is an arbitrary percentage e.g., 50%) multiplied by the degrees above T_b (T-T_b). θ_H represents the difference between the water potential of the environment (ψ) and the minimum ψ required for germination of a specific seed fraction ($\psi_b(g)$) multiplied by time to germination of the g fraction (t_g). $\psi_b(g)$ is assumed to vary across individual seeds in a population, which results in a distribution of germination under conditions where ψ is less negative than $\psi_b(g)$. Recall water potential is a negative value and differences between ψ and $\psi_b(g)$ tend toward zero as full germination of the fraction is prompted.

The hydrothermal time approach combines these two frameworks and describes progress towards germination using equation (2) below:

$$\theta_{HT} = (T\text{-}T_b)(\psi\text{-}\ \psi_b(g))\mathrm{t}_g \qquad (2)$$

where θ_{HT} is the hydrothermal time a seed requires for germination (MPa ° d), T_g is the time to germination of the g fraction, T is the temperature of the medium, T_b is the base temperature below which germination does not occur, ψ is the water potential of the medium, and ψ_b is the water potential below which germination of the entire g fraction will not occur. θ_{HT} and T_b are assumed to be constant for a seed population, while $\psi_b(g)$ and t_g vary with germination fraction, so that it is likely that some seeds do germinate when ψ of the media is less than $\psi_b(g)$, but within some range of conditions typically described as the standard deviation of $\psi_b(g)$. ψ_b values are assumed to have a normal distribution, with a mean $\psi_b(50)$ and standard deviation $\sigma\psi_b$. This normal distribution generates the cumulative inverse normal distribution of t_g seen in germination time course series.

Analysis

Cumulative germination maximums (*gmax*) were calculated from the growth chamber trial data (maximum germinant per petri dish / number of seeds sown per petri dish), and represent the highest cumulative germination achieved among all treatments. To calculate θ_{HT}, $\psi_b(50)$, T_b, T_c, and $\sigma\psi_\mathrm{b}$, germination time course data was analyzed by repeated probit regression using an Excel program written by S. Liu and K. J. Bradford (Gummerson 1986, Bradford 1990, 2005, Alvarado and Bradford 2002). To estimate the cardinal temperatures T_b and T_c, only data from the -.025 MPa treatment was used. T_b is considered constant for a seed population, while T_c is estimated as $T_c(50)$. Germination rates (GR(g)) were calculated as the inverse of time to a specific germination fraction ($1/t_g$). We compared species using GR(25) due to the poor performance of the seed population approaching the 50th percentile. $\psi_b(50)$ presented in Table 2 were the lowest out of all temperature groups.

To examine the relationships between germination traits we used the species mean values resulting from the germination analysis (*gmax*, $\psi_b(50)$, T_b, T_c) and performed Principal Components Analysis (PCA). Pearson's correlation coefficients (r) were calculated as well, to help identify possible relationships to known vegetative traits relative growth rate (RGR) and intrinsic water use-efficiency (WUE). Principal components analysis was performed in R using the factoextra package (Kassambara 2017).

To determine which traits may serve as predictors of drought response, we performed a multivariate step-wise regression analysis of a select group of germination traits (informed by the PCA and vegetative-germination trait correlations) against log response ratio values from the West Loma Ecological Restoration Experiment (Kimball 2017).

Results

The species in this study varied in the fraction of viable seeds in their seed crop as estimated prior to our hydrothermal germination trials by tetrazolium staining (with dormancy breaking of un-germinated fractions using GA3 where necessary). Of the shrub species, *Salvia apiana* had over 80% seed crop viability, while the value for *Eriogonum fasciculatum* was quite low (<15%). *Stipa pulchra*, the perennial grass in the study, had fairly high viability at 60%, while the two forbs (*Chaenactis artemisifolia* and *Salvia columbariae*) has values less than 40% (Table 2). The cumulative maximum fraction of viable seeds (*gmax*) that germinated in the growth chambers ranged from 27.19% - 85.16% (Fig 1A). Temperatures in which *gmax* were achieved differed among species. The majority of *gmax* were reached at 14°C with the exception of the greater lower temperature performance of *C. artemisifolia* (gmax occurred at 8°C), and the greater high temperature performance of *S. apiana* and *S. pulchra* (gmax occurred at 22°C). There was no clear relationship between viability determined with tetrazolium staining and *gmax* observed across species from our germination trials.

GR(25) increased linearly between T_b and the optimal treatment temperature (T_{opt})(defined here as that temperature which supported the highest documented germination), and decreased between T_{opt} and T_c, in all species (Fig. 2). Germination rate generally decreased with ψ. GR(25) at -0.025 MPa and T_{opt} ranged from 0.036 in *C. artemisifolia* to 0.185 for *Salvia apiana* (Table 2).

Data on germination timing in the hydrothermal experiment served to provide good fits for the production of thermal time models (Table 2). Only *Salvia apiana, Salvia columbariae,* and *Salvia mellifera* resulted in low goodness of fit in the thermal time analysis (Table 2). Among our study species, the range of θ_T was fairly narrow (86.16 - 107.28 °hours), with *Chaenactis artemisifolia* having the longest time values, while *Artemisia californica* had the shortest time values. In comparison to the thermal time model, the hydrothermal model fit the data for suboptimal temperatures well for all species (Table 2). In this case, the analysis resulted in a much wider range of values: θ_{HT} varied from 2819.3 MPa°hours, in *Stipa pulchra* to 8000 MPa°hours in *Encelia californica, Eriogonum fasciculatum*, and *Isocoma menziesii.*

$\psi_b(50)$ values ranged from essentially 0 MPa in *Chaenactis artemisifolia* and *Salvia. columbariae* to -1.91 MPa in *Isocoma menziesii* (Fig. 1C). In general, $\psi_b(50)$ increased with T, with extremely mesic conditions required to germinate 50% of the seed population for some species. $\sigma\psi_b$, an indicator of the uniformity of germination, varied widely, ranging from 0.73 MPa in *Chaenactis artemisifolia* to 2.15 MPa for *Isocoma menziesii*. Higher $\sigma\psi_b$ values represent a higher variation in the germination timing across individual seeds within the population of seeds tested for a species (Allen 2000). Cardinal temperature T_b and T_c (presented as $T_c(50)$) were estimated for all species. T_b values were almost all 1°C, with the exception of *Isocoma menziesii*, *Salvia apiana*, and *Stipa pulchra* (1.9°C, 4°C, and 4.5°C respectively) (Fig 1B) and T_c values ranged from 20°C-38°C (Fig 1B). $T_c(50)$ was lowest for *Chaenactis artemisifolia* and highest for *Salvia apiana*. We found one significant correlation when comparing among germination traits: *gmax* was negatively correlated with $\psi_b(50)$ so that *gmax* increases as $\psi_b(50)$ becomes more negative.

Within our sample group, $\Delta^{13}C$ ranged from 16.96 per mil for *Salvia apiana* to 22.58 per mil for *Stipa pulchra*. *Encelia californica* had the lowest RGR at 0.055 g g-1 d-1, while *Artemisia californica* had the highest (0.083 g g-1 d-1). Seed mass varied from 0.007 g in *Artemisia californica* to 0.326 g in *Stipa pulchra* (Table 2). There were a number of correlations when comparing germination traits against vegetative growth and water-use traits: *gmax* was negatively correlated with $\Delta^{13}C$, while positively correlated with $\psi_b(50)$. RGR was negatively correlated with T_c and positively correlated with $\psi_b(50)$(Table 3). Additionally, seed mass was positively correlated with T_b and $\psi_b(50)$. Differences among species were largely explained by two PC axis, including germination maximum, T_b, T_c, and $\psi_b(50)$, RGR, and Δ13C. PC1, which explained 55.7 % of the variation, was associated with $\psi_b(50)$, RGR, and *gmax* and PC2, which captured 29.6% included the variation of Tb, Tc, and WUE (Fig 3).

Log response ratio (rr) values, as included in Kimball 2017, identified species that lost vegetative cover during the three-year drought (negative rr values), and others that increased cover (positive rr values). The entire range of response values extended from -2.085 (*Salvia columbariae*) to 2.994 (*Isocoma menziesii*). When we investigated the potential power of certain functional traits to explain vegetative cover increase, a model consisting of only $\psi_b(50)$ and $\Delta^{13}C$ predicted the log response ratio best (R^2 of .8575, adjusted R^2 = .7625, p=.0538)(Fig 4.) even though the model suggested by our step-wise regression included $\psi_b(50)$, $\Delta^{13}C$, and T_c (Table 4). A combination of less negative base water potential and higher WUE were associated with greater performance through the extended drought.

Discussion

Comparing germination response to temperature and water potential among a group of species that vary in life form contributes to a more complete understanding of regeneration in complex systems characterized by environmental variation, and germination ecology in general (Bradford 2002, Barga 2017, Long et al 2015, Grubb 1977). By examining germination in combination with other important physiological traits, we also strengthen our understanding of the underlying mechanisms associated with plant strategies (Adler et al 2014). Here we described among species variation in key germination traits (Fig. 1) and links between germination and vegetative traits related to growth and water-use (Table 3). Specifically, we find that species with low $\psi_b(50)$ have high WUE, low θ_T, and germinate high fractions while those with high $\psi_b(50)$ have low WUE, high θ_T and germinate low fractions. Similar traits strongly influence long-term population dynamics in arid annual systems (Huang et al. 2016) and we provide evidence that these traits may partially underlie vegetation response to drought by identifying both $\psi_b(50)$ and WUE as potential predictors of how vegetative cover might change during periods of environmental stress, results that make intuitive sense in the context of extreme water limitation (Flores & Briones 2001, Tardieu 2011).

A seed population represents a group of unique genotypes (Forcella 2000) that may differ in their response to temperature and water potential (Bradford 1995). θ_T quantifies progress made towards germination in the sub-optimal T range at constant ψ. θ_{HT} quantifies progress made towards germination over a range of sub-optimal T and ψ, once minimum thresholds have been met. In both cases, distribution of $\psi_b(g)$ values results in the inverse normal distribution of germination time series curves. Low θ_T and more negative $\psi_b(50)$ have been shown to correlate with "fast" germination resulting in high germination fractions in annual forb communities (Huang et al. 2016). Considering the more complex assemblage of life forms in CSS, we expected these germination characteristics to associate with perennial species instead, and they did. θ_T was lowest among perennial shrubs, and highest in the annual forb *Chaenactis artemisifolia.* It should be noted that we were unable to calculate θ_T for three species, primarily due to low germination fraction (Table 2). Upon estimation, we found annual forbs and perennial bunchgrass had lower θ_{HT} (i.e. make faster progress towards germination at suboptimal T and ψ's) compared to perennial shrubs (Table 2), which is due to their higher $\psi_b(50)$ and lower $\sigma\psi_b$ values. Only one shrub, *Salvia mellifera*, had a fairly high $\psi_b(50)$. Taken together, these data suggest that shrubs have traits that support their germinating faster than other CSS life forms as ψ of soil becomes less negative. Additionally, shrubs may be the life form more likely to germinate on average as they have the ability to perform in the more negative ψ range (Fig. 1C).

These results make sense when considered in the context of plant strategies that ecologists have long used to organize species, and the functional traits that underlie their evolution

(Mac Arthur & Wilson 1967, Grime 1977, Wright 2004, Adler 2014). In unpredictable environments, examining how plant traits co-vary provides insight on strategies for coping with constraints such as water limitation. Certain species tend to avoid drought stress, while others have adapted to tolerate it (Gutschick 1987, Smith, Monson, and Anderson 1987, Kimball 2017). In this case, certain species have traits we might expect in drought avoidance: high $\psi_b(50)$, low *gmax,* high $\theta_{T,}$ high WUE. Conversely, other species possess traits we might associate with drought tolerance: low $\psi_b(50)$, high gmax, and low θ_T have high WUE (Table 2).

How important are these traits for predicting ecological dynamics? Here we found species that were able to increase vegetative cover during drought were similar in their low $\psi_b(50)$, high $\sigma\psi_b$, high *gmax*, and high WUE (the majority of species with these traits also had high θ_{HT} though exceptions were noted). Some of these species also had small seeds, but not all, and in general, there were no clear relationships between seed size and drought. The positive correlations between $\psi_b(50)$ and $\Delta^{13}C$, along with those between $\psi_b(50)$ and RGR, suggest that species which germinate in dry conditions may also be stress tolerant, which makes intuitive sense (Angert 2007, Huxman 2013). However, not all species with these germination traits had high WUE and low RGR. *Eriogonum fasciculatum,* which also increased cover during drought, has low WUE and high RGR. *Artemisia californica* had the highest RGR of the group, though it was coupled with high WUE. Species that did not increase cover during drought were similar in their high $\psi_b(50)$ (0.0 MPa - -0.11 MPa), low $\sigma\psi_{b,}$ and low WUE. Overall, recruitment opportunities may be limited to wet years and more mesic microsites for these species, which included the annual forbs

Chaenactis artemisifolia and *Salvia columbariae,* and the perennial bunchgrass *Stipa pulchra*. Unfortunately, we lack drought response data for *Salvia mellifera*, the only perennial shrub that shared these characteristics, as well as *Chaenactis artemisifolia*.

Elner (1987) described germination of a high fraction of seed as a high-risk strategy that results in success during favorable years but failure during times of stress, but it's possible this trait, in conjunction with low ψ(50) and high WUE, confers some advantage during extended periods of drought for certain species. During extended drought, the ability to germinate when other species may be dormant could result in establishment during 'competition free' periods with relatively low plant densities and a greater probability of survival. This reinforces the idea that to truly determine the influence of functional traits on the evolution of plant life history strategies, numerous traits across life cycle phases must be considered (Adler et al. 2014, Westoby 2002). Significant progress has been made in describing above-ground vegetative trait schema that underlie patterns of variation in plant communities (Westoby 1998, Westoby 2002, Wright 2004) and more recently, connections between above and below ground traits have been described (Morales et al. 2014). Below ground trait spectra that contribute to plant performance under stressful conditions (Larson and Funk 2016) and those that influence ecosystem level processes, have also been identified (Bardgett 2017). Recent work by Huang et al. (2016) has described the link between regenerative and vegetative traits, yet the synthesis of reproductive, below-ground, and root traits that support seedling establishment is as yet incomplete.

In conclusion, our study helps to further our understanding of plant strategies associated with environmental variation by highlighting key functional traits that may confer tolerance to environmental stress. Specifically, we identify $\psi_b(50)$ and WUE as two traits that may support persistence through drought. To advance our study, we would suggest further experimentation on a wider set of CSS species over a full range of environmental conditions, and additional research that explores the role of seed production and dispersal in maintaining seed inputs. Synthesis of these results within the context of long term demographic data will help us better understand the role of the regeneration phase in mediating population dynamics and further define strategies that support community resilience in the face of changing environmental conditions.

Tables

Table 1: Native plant species used in the study.

Species	**Family**	**Life form**	**Habit**	**Species Code**
Artemisia californica	Asteraceae	Perennial	Shrub	ARTCAL
Chaenactis artemisifolia	Asteraceae	Annual	Forb	CHAART
Encelia californcia	Asteraceae	Perennial	Shrub	ENCCAL
Eriogonum fasciculatum	Polygonaceae	Perennial	Shrub	ERIFAS
Isocoma menziesii	Asteraceae	Perennial	Shrub	ISOMEN
Salvia columbariae	Lamiaceae	Annual	Forb	SALCOL
Salvia apiana	Lamiaceae	Perennial	Shrub	SALAPI
Salvia mellifera	Lamiaceae	Perennial	Shrub	SALMEL
Stipa pulchra	Poaceae	Perennial	Grass	STIPUL

Table 2: Values of germination, growth, and water-use traits and other data from the germination trials.

Plant species	ARTCAL	CHAART	ENCCAL	ERIFAS	ISOMEN	SALAPI	SALCOL	SALMEL	STIPUL
#seeds used in germination trial	100	150	75	200	125	50	50	50	75
Viability of seed population (%)	0.32	0.38	0.60	0.14	0.21	0.87	0.24	0.21	0.60
GR(25) maximum at -0.025 MPa	0.133	0.036	0.080	0.117	0.087	0.185	0.046	0.068	.126
Temperature for estimating GR(25) (°C)	14	8	14	14	14	22	14	22	22
T at which gmax was reached (°C)	14	8	14	14	14	22	14	22	22
Seed mass (g)	0.007	0.037	0.114	0.044	0.058	0.173	0.120	0.067	0.326
Standard error of seed mass	0.004	0.021	0.066	0.025	0.034	0.099	0.069	0.039	0.182
θT (° hours)	86.16	107.28	96.96	95.52	92.16	-	-	-	97.68
Standard error of θT	0.32	0.82	0.53	0.46	0.43	-	-	-	0.65
θT R^2	0.953	0.811	0.886	0.791	0.942	-	-	-	0.911
θHT(MPa ° hours)	6100	3396	8000	8000	8000	3569.4	3121	5057	2819.3
θHT R^2	0.892	0.932	0.895	0.739	0.823	0.787	0.888	0.929	0.931
$\psi_b(50)$ (MPa)	-1.57	≈0	-0.39	-1.30	-1.91	-0.73	≈0	-0.09	-0.11
Standard error of $\psi_b(50)$	1.23	0.73	2.05	1.54	2.15	1.05	0.90	0.93	0.90

Condition for estimating $\psi_b(50)$ (°C)	14	14	8	14	8	8	14	14	22
$\Delta^{13}C$ (per mil)	17.84	-	19.12	19.44	-	16.96	21.80	-	22.58
Standard error of $\Delta^{13}C$	0.12	-	1.06	0.22	-	0.79	0.08	-	0.35
Relative growth rate g g-1 d-1 (RGR)	0.083	-	0.055	0.078	0.057	0.061	0.069	0.067	0.058
Standard error of RGR	0.009	-	0.009	0.004	0.008	0.007	0.013	0.007	0.010
PC1 Score	-2.881	-	0.955	-1.425		0.169	1.166	-	2.016
PC2 Score	-0.043	-	-0.036	-0.252	-	2.492	-1.453	-	0.007
Log response ratio (rrdrought)	1.582	-	1.132	1.909	2.994	1.940	-2.085	-	-1.234

Table 3: Correlation analysis with Pearson's correlation coefficients and p-values.

Variable 1	Variable 2	Pearson's r	p-value
Gmax	**$\psi_b(50)$**	-0.84	0.0342
Gmax	**$\Delta^{13}C$**	-0.77	0.0726
$\psi_b(50)$	**$\Delta^{13}C$**	0.69	0.128
T_c	**RGR**	-0.71	0.116
$\psi_b(50)$	**RGR**	0.77	0.071
$\psi_b(50)$	**Seed Mass**	0.77	0.071
T_b	**Seed Mass**	0.84	0.018

Table 4: Two way step-wise regression to determine germination functional traits that serve as possible drought response predictors.

Start: AIC= 1.76	Df	SS	RSS	AIC
rrdrought ~ $\psi_b(50)$ + T_c + T_b + Δ13C				
(-) T_b	1	0.02683	1.5461	-0.1361
(-) Δ13C	1	0.56164	2.0809	1.6463
(-) T_c	1	0.58200	2.1013	1.7048
<none>				
(-) $\psi_b(50)$	1	1.56398	3.0833	4.0054
Step: AIC=0.14				
rrdrought ~ $\psi_b(50)$ + T_c + Δ13C				
<none>			1.5461	-013607
(-) T_c	1	0.63536	2.1815	-0.07055
(-) Δ13C	1	0.67618	2.2223	0.04068
(+)T_b	1	0.02683	1.5193	1.75891
(-) $\psi_b(50)$	1	1.54256	3.0887	2.01591
Final Model: rrdrought ~ ψb(50) + Tc + Δ13C				

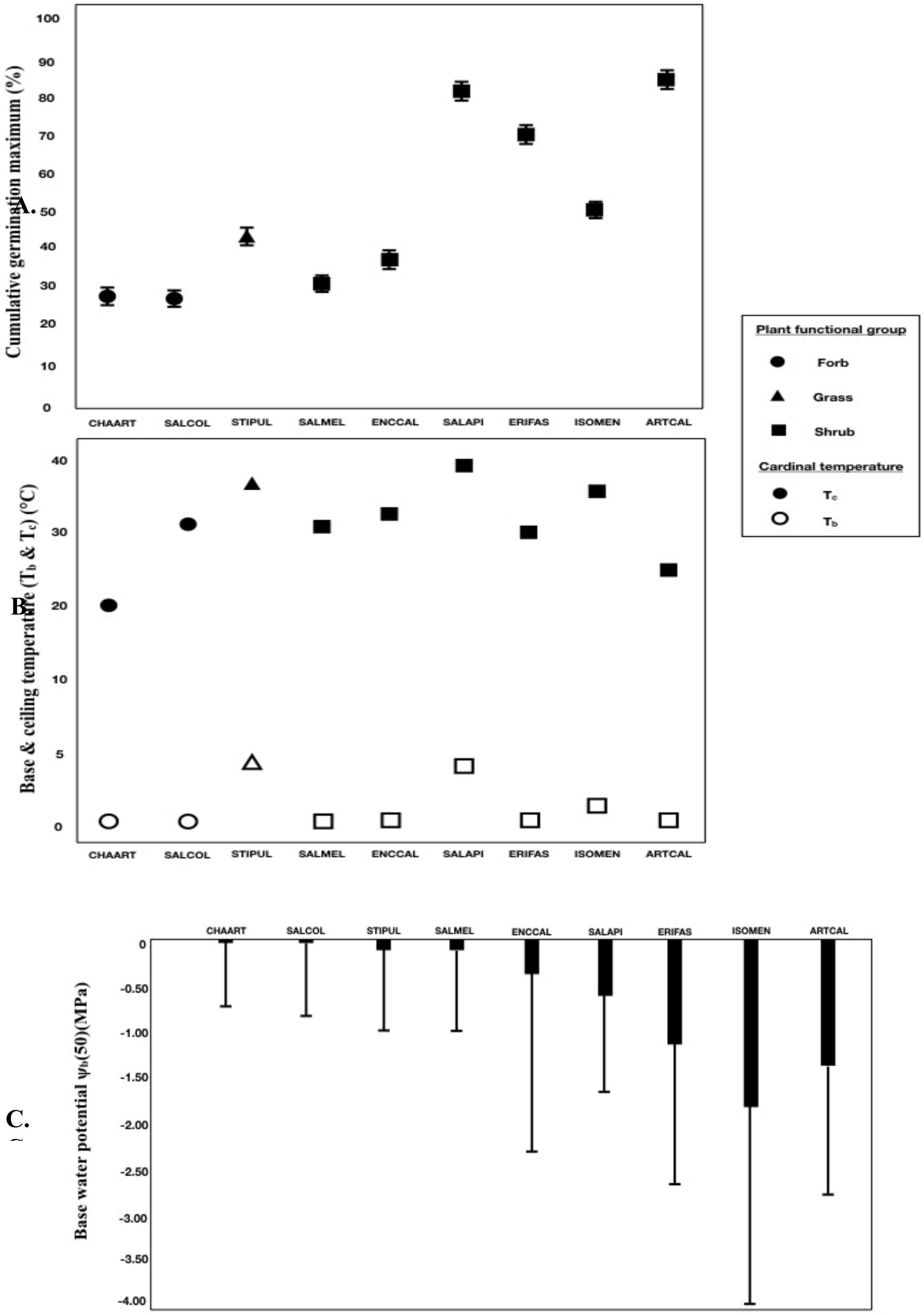

Figure 1: **Species mean values of germination functional traits**. Cumulative germination maximum (*gmax*) of forbs, grasses, and shrubs (panel A); base temperature required for germination (T_b) & ceiling temperature above which 50% germination does not occur ($T_c(50)$) of these same plant species (panel B); base water potential required for 50% germination fraction ($\psi_b(50)$) - error bars represent standard error of base water potential ($\sigma\psi_b$). (panel C).

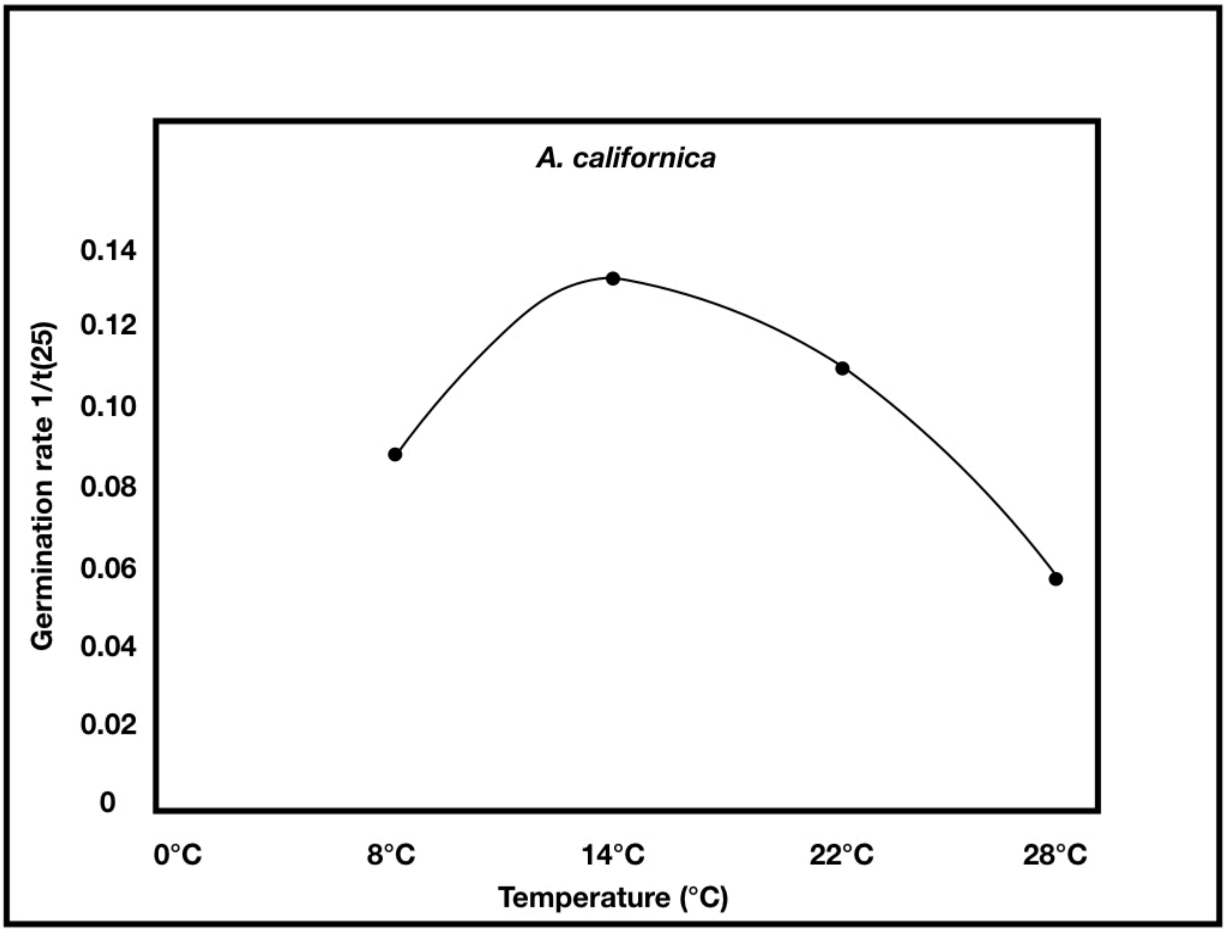

Figure 2. Relationship between germination rate of the 25% fraction (GR(25)) and temperature for the perennial shrub *Artemisia californica*. Germination rate (GR) defined as 1/t(g), increases between base temperature required for germination (T_b) and optimal temperature for germination (T_{opt}) and decreases between T_{opt} and ceiling temperature above which 50% of the seed population does not germinate (T_c(50)).

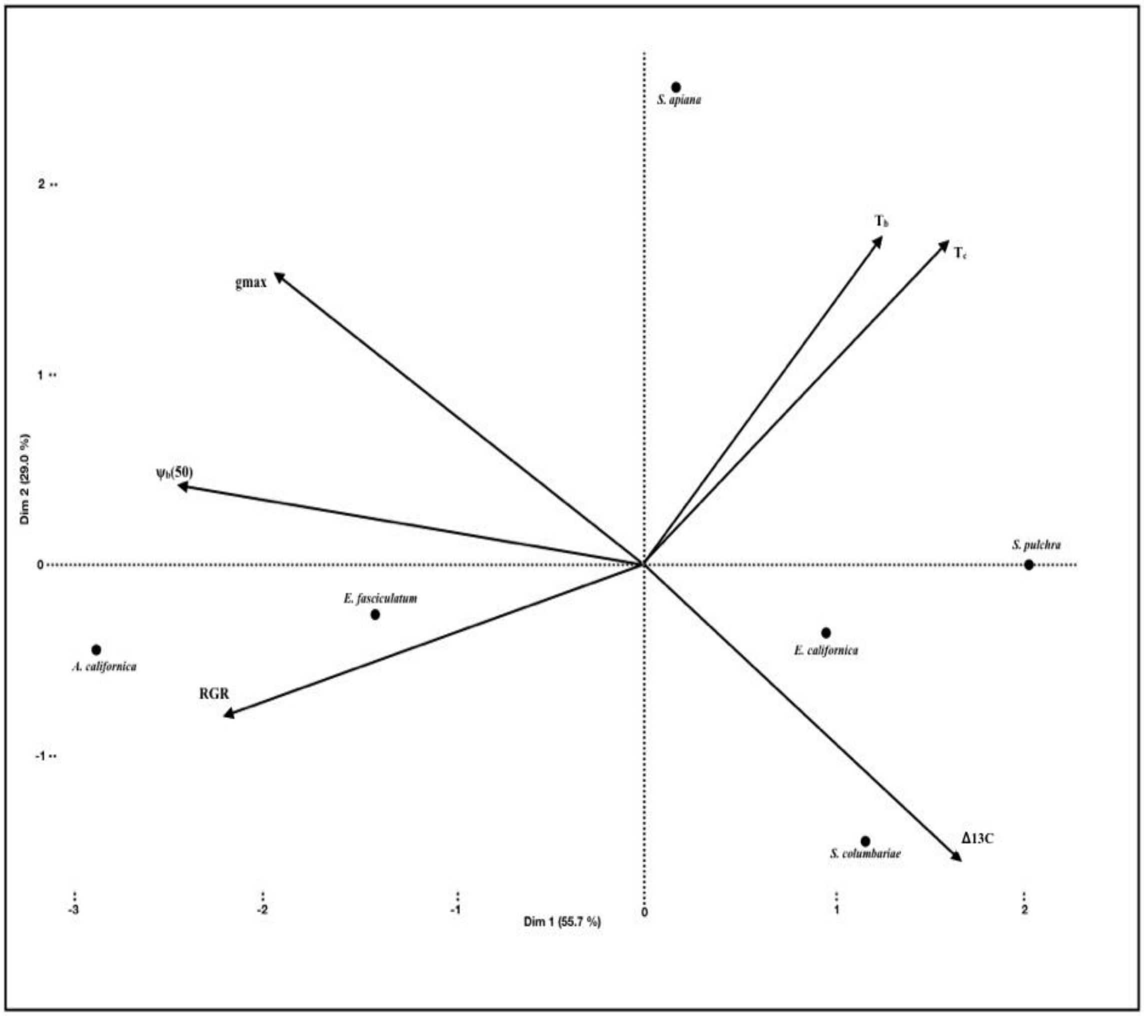

Figure 3: Principal components analysis for visualizing plant functional traits related to germination, growth and water-use. Traits include cumulative germination maximum (*gmax*), base water potential required for 50% germination ($\psi_b(50)$), relative growth rate (RGR), carbon isotope discrimination ($\Delta^{13}C$), base temperature required for germination (T_b), and ceiling temperature above which 50% germination does not occur ($T_c(50)$).

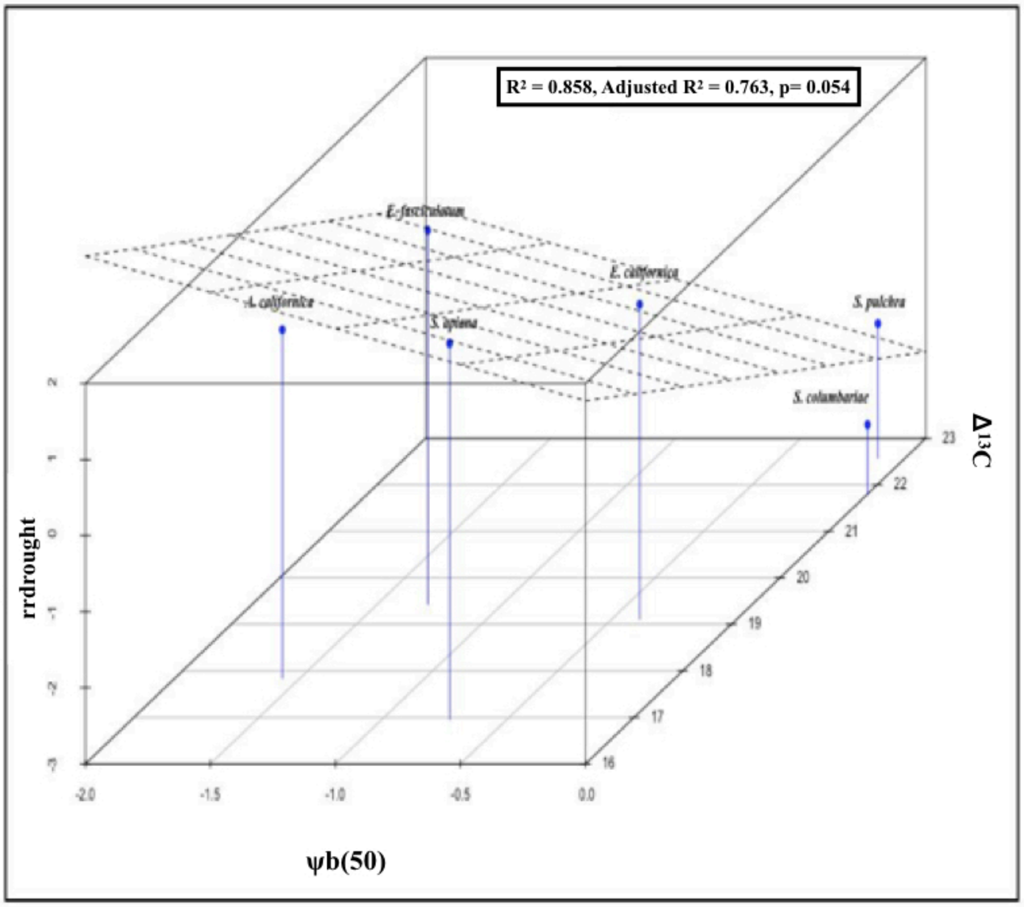

Figure 4: Multivariate regression of rrdrought ~ $\psi_b(50)$ + $\Delta^{13}C$. The log ratio response values representing the change in vegetation cover of plant species over a 3-year drought in Orange County, CA are represented by rrdrought. Predictors of this change in vegetation include base water potential required for germination of the 50% fraction ($\psi_b(50)$) and integrated water use efficiency measured as carbon isotope discrimination ($\Delta^{13}C$).

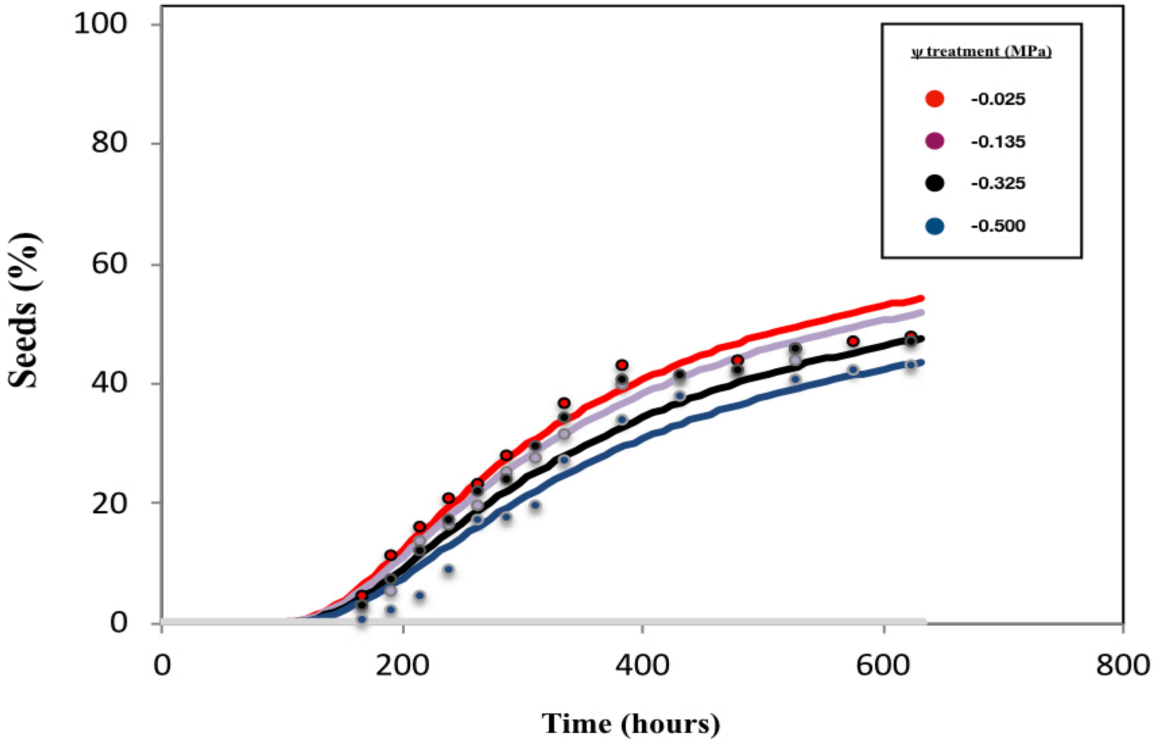

Figure 5: Germination time-course series predicted for *Isocoma menziesii* by hydrothermal model. Example figure representing germination time course series of observed data (points) and those predicted by the hydrothermal time model (lines) at 14°C and four ψ treatments (-0.025 MPa, -0.135 MPA, -0.325 MPa, -0.50 MPa). Model $R^2 = 0.739$.

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