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ORIGINAL PAPER

Germination response to temperature and moisture to predict distributions of the invasive grass red brome and wildfire

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Abstract The annual grasses red brome (*Bromus rubens* L.) and cheatgrass (*Bromus tectorum* L.) are associated with increased frequency and size of wildfires in the Great Basin and Mojave deserts of North America. Invasion success of these exotic grasses is driven in part by germination responses to climate fluctuations. Understanding how climate influences germination characteristics of invasive grasses is critical to predicting desert wildfire. While the germination characteristics of cheatgrass have been reported, the germination requirements for red brome, the exotic grass associated with fire in the Mojave Desert, have not. Herein we characterize germination response of red brome through hydrothermal-time modeling. The hydrothermal-time requirements were matched with historic climate data to estimate optimal germination periods for red brome and its potential association with wildfire. The optimal temperature for germination in a population of red brome seeds was 19.3 °C with a hydrothermal-time constant of 38.9 MPa °C days and a mean base water potential of −1.35 MPa. Based on the hydrothermal model, high red brome germination rates are most likely to occur in wet Octobers when optimal fall temperatures overlap with adequate moisture. Abnormally high precipitation totals in the fall of 2004 created ideal conditions for red brome germination that likely contributed to the large-scale Mojave Desert fires of 2005. Predicted intensification of fall and winter precipitation events in response to climate change will likely drive further increases in red brome abundance and subsequently more widespread fire in regions of the Mojave Desert.

Keywords Brome · Invasive grass · Fire regime · Ecosystem transition · Mojave Desert

Introduction

Invasion by exotic plants can fundamentally alter plant communities by competing for resources and altering disturbance regimes (Chapin III et al. 2000). Exotic grass invasions are associated with changing fire regimes in arid ecosystems (D'Antonio and Vitousek 1992). Exotic grasses fill in inter-shrub spaces creating continuous fuels that contribute to larger and more frequent wildfires (D'Antonio and Vitousek 1992; Brooks 1999; D'Antonio 2000). Many desert plant species are not adapted to fire, while exotic grasses tend to respond positively to fire, and may promote the transition of desert shrublands to exotic grasslands (Callison et al. 1985; Zouhar et al. 2008; Vamstad and

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Rotenberry 2010; Engel and Abella 2011; Brooks 2012).

The annual grasses red brome (*Bromus rubens* L.) and cheatgrass (*Bromus tectorum* L.) have invaded vast areas of western North America (Reid et al. 2008). Success of *Bromus* spp. invasion is driven by functional strategies that include rapid growth rates, drought avoidance, high propagule pressure, positive responses to disturbance including fire and low moisture requirements for germination (Beatley 1966; Wu and Jain 1979; Salo 2004). In contrast to native species these exotic grasses have faster growth rates, are positively affected by fire (Angert et al. 2007), and have more flexible germination requirements (Wallace 1972; Reynolds et al. 2012). The presence of exotic *Bromus* grasses can drastically reduce fire return intervals in the Mojave and Great Basin Deserts and dramatically increases fire size (Brooks et al. 2004; Reid et al. 2008; Brooks 2012).

The growth and expansion of red brome and cheatgrass is strongly controlled by weather conditions (Salo 2005; Chambers et al. 2007; Reid et al. 2008) that are highly variable in arid and semi-arid deserts (Hereford et al. 2006; Snyder and Tartowski 2006). Historically, expansions of red brome have coincided with 'warm' Pacific Decadal Oscillation regimes and future expansions are likely to respond to anthropogenic changes in global climate patterns (Loik et al. 2004; Salo 2005). Fall precipitation events are positively associated with relatively high abundances of red brome (Beatley 1976; Abella et al. 2012). Early fall precipitation events likely promote brome germination (Abella et al. 2012) since summer and winter temperature extremes may inhibit seed germination (Alvarado and Bradford 2002).

Sensitivity to high temperatures prevents seeds from germinating during the summer season when precipitation is unpredictable and soil moisture does not persist (Alvarado and Bradford 2002; Huxman et al. 2004; Potts et al. 2006). However, high summer temperatures are necessary to overcome primary dormancy in *Bromus* seed (Bradford 2002; Meyer and Allen 2009). Prolonged exposure to high temperatures gradually decreases the level of dormancy in seeds of *Bromus* spp. resulting in increased responsiveness to a wider range of temperatures and moisture (Allen et al. 1995).

Temperature and seed zone moisture are the primary drivers for seed germination in many plant species and can be described using hydrothermal-time models (Gummerson 1986; Bradford 1995; Allen et al. 2000). Investigation of germination characteristics using hydrothermal-time models has led to accurate predictions of germination in the field of onions, carrots (Rowse and Finch-Savage 2003), and cheatgrass (Roundy et al. 2007; Meyer and Allen 2009). Knowledge of the germination requirements for red brome, an alien grass linked to increased fire in the Mojave Desert (Beatley 1966; Hunter 1991; Brooks 1999), can be used to predict germination under different climate scenarios that are likely to promote red brome growth and fire risk.

The strong association of the exotic grass red brome to unprecedented wildfires in the Mojave Desert has created the need for greater understanding of red brome biology (Brooks 1999; Brooks et al. 2004; Reid et al. 2008). The objective of this study was to produce a hydrothermal-time model that accurately characterizes germination requirements for a population of fully after-ripened seeds of red brome, and then identify weather patterns that influence germination and potential associations these patterns had with historic fires. We predicted that red brome germination rates are optimal at temperatures and water potentials observed during wet fall periods in the Mojave Desert.

Methods

Site description

The Beaver Dam Wash (37.15°N, 114.01°W) is located in the northeastern corner of the Mojave Desert. The Mojave Desert is classified as a warm desert and receives most of its precipitation in the winter. Vegetation is typical of Mojave Desert mid-elevation (~1,000 m) shrubland dominated by creosote bush (*Larrea tridentata* (DC) Cov.), blackbrush (*Coleogyne ramosissima* Torr.), and white bursage (*Ambrosia dumosa* (A. Gray) Payne) with frequent Joshua trees (*Yucca brevifolia* Engelm.). The exotic annuals red brome (see Horn et al. unpublished data) and red-stem filaree (*Erodium cicutarium* (L.) L'Hér. ex Aiton) are prevalent on the landscape. Fire has historically been rare in the Mojave Desert however, the region has experienced several fires since 1984 with the fires of 2005 having burned more area than all previous fires combined (Brooks and Matchett 2006).

Seed collection and incubation

Mature and senescent red brome stems with attached seeds were collected along a single plateau within Beaver Dam Wash (37.148N, 114.014W) in May of 2011. Seeds were stored at room temperature (~20 °C) until October at which time they were stripped from stems and counted. Seeds were then incubated at 40 °C for 48 h. Germination results indicated that the seeds had become non-dormant.

To observe germination responses, 25 red brome seeds were incubated in petri dishes on germination blotters (Anchor Paper, St. Paul, MN) under a full factorial combination of five different water potentials (0.0, −0.5, −1.0, −1.5, and −2.0 MPa), six different temperatures (0, 5, 10, 20, 25, 30 °C), replicated four times. Temperature control was achieved using six refrigerated incubators (Model 818, Precision Scientific, Buffalo NY). Experimental replication occurred by repeating the experiment across time. Water potentials were obtained using various concentrations of polyethylene glycol (PEG 8000 Sigma Aldrich) based on the equations of Michel (1983) including corrections for temperatures. After solutions were prepared water potentials were recalculated from the measured weights of PEG and water (see Eq. 1).

$$\psi = 1.29T\,[PEG]^2 - 140\,[PEG]^2 - 4.0\,[PEG] \quad (1)$$

Germination blotters were saturated in excessive volumes of PEG solutions to minimize PEG exclusion by the germination blotters (Hardegree and Emmerich 1990). Petri dishes were placed in stacks by temperature treatment and enclosed in a clear plastic bag with a moist paper towel at the top and bottom of each stack to prevent evaporation (Christensen et al. 1996). Stacks were slightly tilted to prevent pooling of PEG solution around seeds. Temperatures were maintained with 12/12 h light cycles. Germinated seeds with radical emergence >1 mm were counted and removed at days 1, 2, 4, 7, 11, 14, 21, and 28.

Hydrothermal-time modeling

We used hydrothermal-time models to characterize germination requirements of red brome collected from Beaver Dam Wash. A fraction of the seed population (g) will progress towards germination by accumulating time ($t_{(g)}$) at temperatures (T) and water potentials (ψ) above a base temperature (T_b) and base water potential ($\psi_{b(g)}$) (Gummerson 1986) that are specific to the population and dormancy condition (Beckstead et al. 1996). The time and base water potential vary with the fraction of the seed population (g) considered. The required amount of time spent above base temperature and water potential is called hydrothermal-time (θ_{HT}) and is a constant value for each population of seeds (Eq. 2).

$$\theta_{HT} = \left(\psi - \psi_{b(g)}\right)(T - T_b)t_{(g)} \quad (2)$$

As both temperature and soil moisture increase above minimum values, the rate of germination ($t_{(g)}^{-1}$), and fraction of germinated seeds (g), also increase until the optimal temperature (T_o) for germination is reached (Gummerson 1986). Above the optimal temperature (T_o) the rate of germination decreases and amount of water required for germination, the adjusted base water potential ($\psi_{b(g)} + k_t(T - T_o)$), increases until the germination rate reaches zero (Eq. 3) (Alvarado and Bradford 2002).

$$\theta_{HT} = \left[\psi - \left(\psi_{b(g)} + k_t(T - T_o)\right)\right](T_o - T_b)t_{(g)} \quad (3)$$

where k_T is the coefficient for the linear increase in base water potential with temperature. The temperature at which the adjusted base water potential equals zero is known as the ceiling temperature ($T_{c(g)}$), above which germination will not proceed for that fraction (g) of the population. The values for base water potential vary with population fraction and are normally distributed about a mean base water potential ($\psi_{b(50)}$) whose standard deviation is denoted by $\sigma_{\psi b}$. Base temperature (T_b) and hydrothermal time (θ_{HT}) are assumed to be constant for the population.

To calculate the hydrothermal-time parameters (θ_{HT}, k_T, T_o, T_b, $\psi_{b(50)}$, and $\sigma_{\psi b}$) for red brome we used repeated linear regression similar to the methods of Christensen et al. (1996) with some differences. The inverse cumulative distribution of the germination fraction [PROBIT (g)] is linearly related to the distribution of the base water potentials (Eq. 4)

$$\mathrm{PROBIT}(g) = m\psi_{b(g)} + b \quad (4)$$

where

$$\psi_{b(50)} = \frac{-b}{m} \quad (5)$$

and

$$\sigma_{\psi b} = \frac{1}{m} \tag{6}$$

and m and b are respectively the slope and intercept of the linear relationship and $\psi_{b(50)}$ is the mean base water potential. Substituting in the full hydrothermal-time equation for $\psi_{b(g)}$ we are able to determine the base water potential ($\psi_{b(g)}$) across both sub-optimal (Eq. 7) and supra-optimal (Eq. 8) temperatures.

$$\mathrm{PROBIT}(g) = m\left(\psi - \frac{\theta_{HT}}{(T - T_b)t_{(g)}}\right) + b \tag{7}$$

$$\mathrm{PROBIT}(g) = m\left(\psi - k_t(T - T_o) - \frac{\theta_{HT}}{(T_o - T_b)t_{(g)}}\right) + b \tag{8}$$

Optimal r^2 values were obtained by manually substituting in values for θ_{HT}, k_T, T_o, and T_b within a spreadsheet application. Input data consisted of data points that had germination fractions greater than 0.05 and less than 0.96.

Climate and fire analysis

To estimate when optimal germination conditions may exist where the seed population was collected, 23 years of temperature data were summarized to means, maxima, and minima by month and precipitation to totals and means for each month for Beaver Dam Wash. Climate data were measured at Badger Springs meteorological station (BADU1 37.1506°N, 113.9539°W, elev: 1,216 m) and Brigham Young University's Lytle Ranch Preserve (MesoWest). Historic fire boundaries were obtained from Monitoring Trend in Burn Severity on-line database (Eidenshink et al. 2007). Seasonality of optimal germination conditions were estimated by comparing optimal germination temperatures to the mean and variance of monthly ambient temperatures.

Results

Germination responses

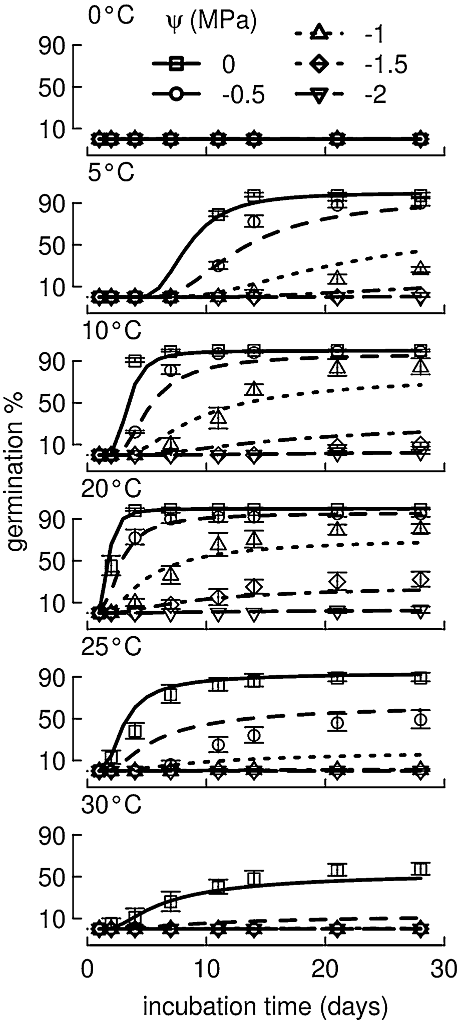

Fig. 1 Germination time courses for a red brome population at 0, 5, 10, 20, 25, and 30 °C. Water potentials shown are approximately 0.0, −0.5, −1.0, −1.5, and −2.0 MPa. Modeled time courses are represented as *lines* with observed means as *points*

Germination rates ($t_{(g)}^{-1}$) appeared to increase above 0 °C, decline above 20 °C, and responded positively to high water potentials (Fig. 1). Temperature regimes fit the overall model from best-fit to least best-fit at 10, 20, 25, 5 and 30 °C with nearly no variation in fit across the temperature values (r^2 values of 0.958, 0.914, 0.910, 0.900 and 0.897 respectively). No seeds were observed to germinate at 0 °C.

Hydrothermal parameters

The hydrothermal-time model with optimized parameters accounted for 83 % of the variation observed in the rate of germination and fraction of germinated

Table 1 Hydrothermal-time parameters for germination of a red brome population

Parameter	Value
Hydrothermal time θ_{HT}	38.9 °C MPa days
Base temperature T_b	1.6 °C
Optimal temperature T_o	19.3 °C
Mean ceiling temperature $T_{c(50)}$	30.5 °C
Mean base water potential $\psi_{b(50)}$	−1.35 MPa
Standard deviation of mean base water potential $\sigma_{\psi b}$	0.41 MPa
Supra-optimal temperature coefficient k_T	0.12 MPa °C^{-1}
r^2	0.83

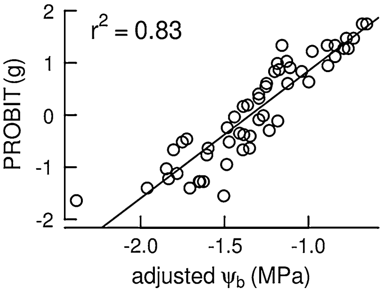

Fig. 2 Linear regression of PROBIT (g) plotted against base water potentials (ψ_b) and adjusted base water potentials ($\psi_b - k_T(T - T_o)$). Points are the mean germination fraction for each set of replicates where $0 <$ germination fraction <0.98

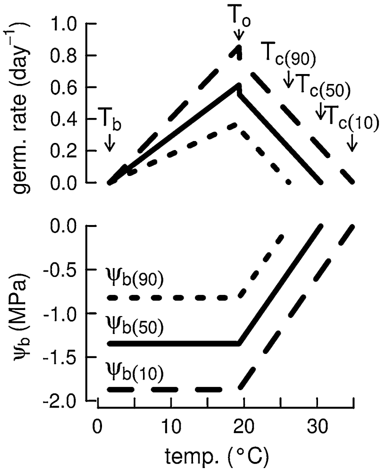

Fig. 3 Germination rates and base water potentials for the 10, 50, and 90 percentile of a red brome population as a function of temperature. Base (T_b), optimal (T_o), and ceiling ($T_{c(10,\ 50,\ 90)}$) temperatures are denoted with *arrows*

seeds (Table 1; Fig. 2). The hydrothermal-time requirement (θ_{HT}) for this population of red brome was 38.9 °C MPa days. Germination progressed towards the hydrothermal-time requirement at temperatures above 1.6 °C(T_b). Rate of germination increased until reaching the optimal temperature (T_o) of 19.3 °C (Fig. 3). Above T_o germination rate declined towards ceiling temperatures ($T_{c(g)}$) at which germination theoretically ceased. Mean base water potential ($\psi_{b(50)}$) increased from −1.35 MPa at temperatures above T_o at a rate (k_T) of 0.12 MPa °C^{-1} until reaching 0 MPa at the mean ceiling temperature ($T_{c(50)}$) of 30.8 °C. Standard deviation of the base water potential ($\sigma_{\psi b}$) was 0.41 MPa.

Beaver Dam Wash climate data

Average monthly temperature in Beaver Dam Wash, where the seeds were collected, was normally distributed while precipitation was severely skewed to large volumes with high inter-annual variability. Minimum and maximum temperatures ranged from −11.7 °C in January to 45 °C in August (Fig. 4). The majority of precipitation received was between the months of October through April but was highly inconsistent from year to year. All calendar months experienced at least 1 year in which no precipitation was received (Fig. 4). The optimal temperature (T_o) for red brome germination was reached in the months of October and April (Fig. 4). However, the mean ceiling temperature ($T_{c(50)}$) was exceeded from April to October. Average precipitation level did not exceeded 5 cm month^{-1}; however, individual months within the past 23 years have accumulated as much as 21 cm precipitation (Dec. 2010). Winter precipitation (Oct.–Apr.) accounted for 75 % of the precipitation received. October of 2004 exceeded 13 cm of precipitation for the month; twice the amount received in any other year.

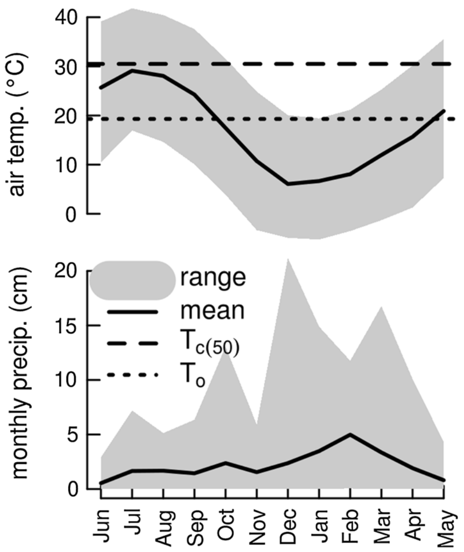

Fig. 4 Monthly range and means for temperature and precipitation for the growing season (June–May) at Beaver Dam Wash between 1989 and 2012. Germination of red brome is optimized when average temperatures is approximately the optimal temperature for germination (T_o, *dotted line*) and maximum temperatures does not exceed mean ceiling ($T_{c(50)}$, *dashed line*) temperatures pending sufficient moisture

Discussion

The observed germination responses (Fig. 1), and derived hydrothermal-time model (Table 1 and Fig. 3), indicated that red brome germination is maximized when (1) appreciable moisture is received to maintain seed available moisture; (2) at times when maximum temperatures do not exceed ceiling temperature ($T_{c(g)}$); and (3) as daily temperature averages near the optimal temperature (T_{o}) for germination. For the northeast region of the Mojave Desert, the temperature requirements are met during the months of April and October (Fig. 4). Both October and April have mean temperatures around the optimal temperature (T_{o}) and mean maximum temperatures less than the mean ceiling temperature ($T_{c(50)}$; Fig. 4). However, in April, seeds in the seedbank from the previous spring are mostly non-viable (Jurand et al. 2013) and red brome plants from the current year are not likely to have senesced and shattered seeds (Kevin Horn, personal observation). Any seeds that have recently shattered would likely have a high degree of primary dormancy (Corbineau et al. 1992; Finch-Savage and Leubner-Metzger 2006). Requirements for dormancy and germination indicate October as the most favorable month in the northeastern region of the Mojave Desert for successful germination pending seed zone receives and maintains sufficient moisture.

We predicted that the expansive fires would have been preceded by conditions that were optimal for red brome germination, which requires appreciable autumn precipitation. Consistent with our prediction, the large 2005 fires in the northeastern Mojave, were preceded by the wettest October on record, exceeding any other year by twice the amount (Fig. 4). The probability of all viable red brome seeds germinating in response to the October 2004 precipitation pulses would have been high (Salo 2004). A 28 year time series of satellite images of the northeast Mojave revealed vegetation greenness was the most intense in spring of 2005 and red brome was a principal component of the vegetation (Horn, unpublished data). October 2010, the second wettest October recorded, also produced increased vegetation greenness and high red brome abundance on the landscape (Horn unpublished data; personal observation). The high abundance of senesced red brome in the Beaver Dam Wash in June 2011 made possible experimental burns that would have easily spread uninhibited if measures had not been taken to control them (Sam St. Clair, personal observation).

Germination responses of red brome show that seeds germinate under a wide range of temperatures (Fig. 1); however, when germination rates are not maximized (i.e. at sub- and supra-optimal temperatures) neither are the odds for germinated plants to survive. One of the risks of germinating at sub-optimal temperatures during the late fall and winter is an increased chance of pathogen infection due to slower germination rates (Beckstead et al. 2007) that reduces the viability of the seedbank (Salo 2004; Jurand et al. 2013). Slower germination rates also occur at supra-optimal temperatures and prevent precocious germination when soil moisture would typically be insufficient to sustain developing seedlings (Alvarado and Bradford 2002; Huxman et al. 2004; Potts et al. 2006).

Variability observed in germination responses (Fig. 1) has important ecological consequences as plant populations respond to variations in inter-annual precipitation. Red brome does not reliably maintain an appreciable seedbank for more than a year (Jurand et al. 2013; Salo 2004); thus successive populations of red brome are largely dependent on seed produced from the previous growing season. However, optimal conditions for germination (i.e. precipitation arriving during optimal germination temperatures) and for subsequent growth may not exist for extended periods of time due to the high inter-annual variability in precipitation (Hereford et al. 2006). Seeds that do germinate under non-optimal conditions, when temperature exceeds or is below the optimal temperature (T_o) (see Fig. 1), potentially generate propagules for the next generation but do so at increased risk of pathogen infection and insufficient moisture for seedling development (Salo 2004; Meyer et al. 2010). Even with the increased risk of plant mortality some plants will potentially reach maturity and set seed. Thus, in the event optimal conditions for germination are not reached during the year, variability in germination increases the odds that the presence of red brome may be maintained on the landscape.

Invading grasses can experience strong selection pressures based on germination traits. Populations of exotic grasses invade and undergo selection in part by how germination characteristics respond to local environmental conditions (Beckstead et al. 1996). This selection is not only evident at the species level, where genotypes of cheatgrass are specific to different invaded regions (Scott et al. 2010; Merrill et al. 2012), but is also demonstrated in niche sorting across the *Bromus* genus. The northern extent of red brome overlaps the southern extent of cheatgrass and coincides with the boundary between the 'cool' Great Basin Desert and the 'warm' Mojave Desert in western North America (Beatley 1966). The germination requirement of each species generally reflects the climate conditions of the environments they have invaded. Specifically, we found that our seed population collected from the northeast Mojave had slightly lower mean base water potential ($\psi_{b(50)} = -1.3$ MPa, $\sigma_{\psi b} = 0.41$ MPa; Fig. 3; Table 1) and lower germination rate ($t_{(g)}^{-1}$; Fig. 3) than cheatgrass populations ($\psi_{b(50)} = -0.81$ to -1.27 MPa) from the Great Basin (Bauer et al. 1998; Bair et al. 2006; Meyer and Allen 2009). Lower mean base water potential indicates red brome seed from this population is capable of germinating in more arid conditions than cheatgrass populations reported in Meyer and Allen (2009). Even though these differences in germination requirements are small, environmental selection, based in part on these differences in germination, has likely led to the current distribution of these *Bromus* species at the boundaries of the Mojave and Great Basin deserts (Beatley 1966; Reid et al. 2008).

Recent expansion of invasive grasses in deserts appears to be linked to climate patterns (Hereford et al. 2006; Brooks and Chambers 2011; Abella et al. 2012). Early fall and sustained winter precipitation generated favorable moisture conditions for germination and growth of red brome (Fig. 4). Germination of red brome in particular is highly responsive to early fall precipitation events that help to maximize abundance of red brome on the landscape (Abella et al. 2012; Horn et al. unpublished data). Early fall rain events occur when temperatures are optimal for red brome germination (Fig. 3) and pending sufficient moisture nearly all viable seeds are likely to germinate (Fig. 1). However, fall and winter precipitation has fluctuated widely from year to year where some months received little to no precipitation (Fig. 4).

Predicted changes in climate will likely favor increased germination and growth in red brome. Climate models for southwestern North America predict an increase of intense fall and winter precipitation events and more frequent and intense drought (IPCC 2007; Jentsch and Beierkuhnlein 2008). Based on our data, greater fall precipitation will increase the proportion of red brome germination (Figs. 1, 2) when fall temperatures are optimal for germination (Fig. 4).

Increased germination in red brome is likely to result in greater fine fuels and vegetation connectivity that promotes fires in the Mojave Desert (Brooks 1999). The spatial extent of fires will likely fluctuate as populations of red brome germinate and grow in response to fluctuating climate conditions (Agnew 1997; Westerling et al. 2003). Years of intense fall and winter rainfall will maximize germination and growth of red brome allowing exotic grass to fill shrub interspaces with fine fuels that carry fire (Brooks 1999; Brooks et al. 2004).

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